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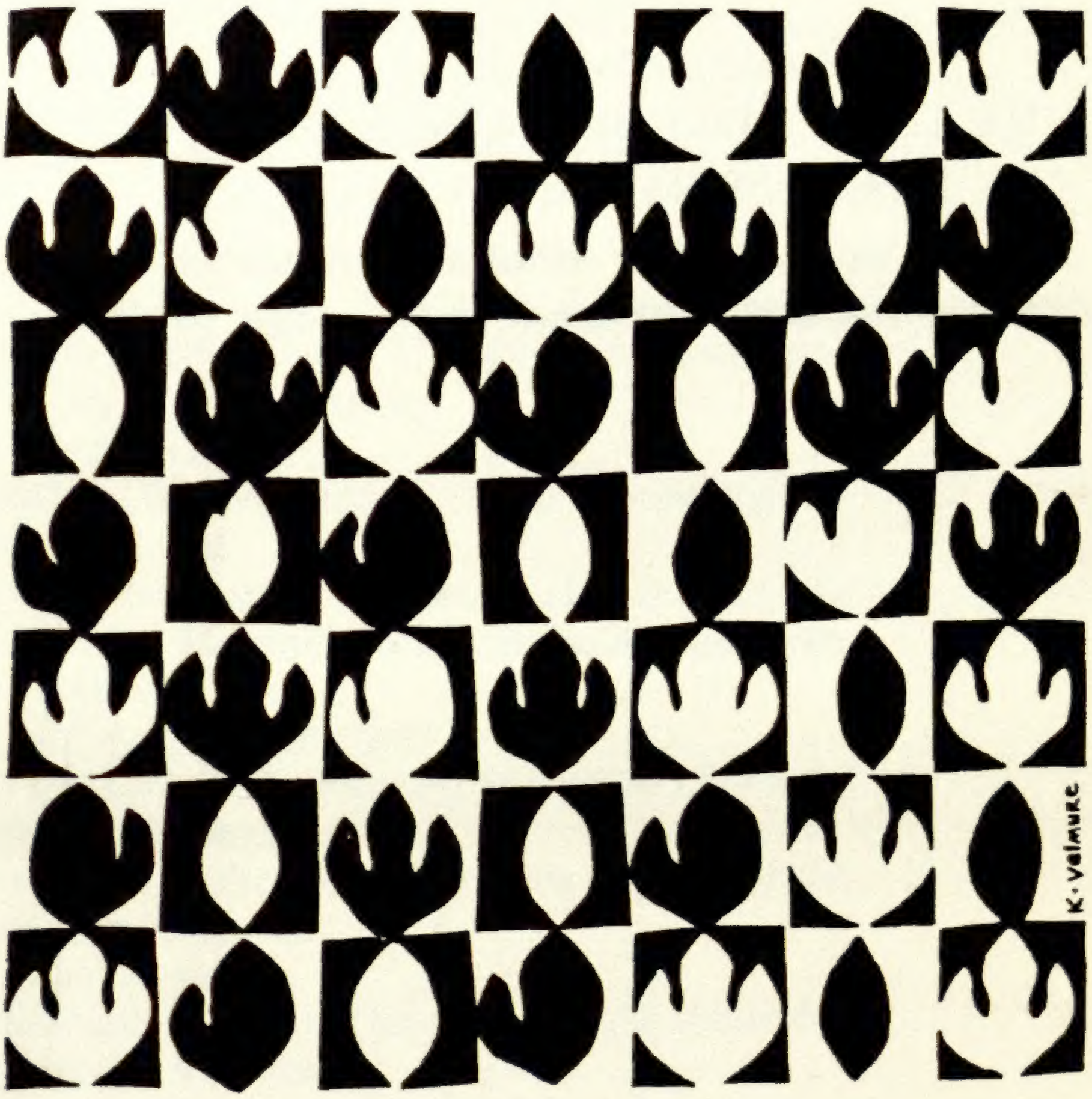

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COVER: A "mass collection" of leaves of *Sassafras albidum* (Nutt.) C. G. Nees, a handsome lauraceous tree of eastern North America and a probable Arcto-Tertiary relict, along with its two living congeners in eastern Asia. Its attractive small, yellow flowers are produced early in the spring as the leaves first unfold. The elliptic leaves, either entire, mitten-shaped, or 3-lobed at apex, become beautifully red-and-yellow colored in autumn. Although sassafras has long been thought to have medicinal properties, it is probably no more than a mild aromatic stimulant. A tea is made from the wood of sassafras roots; from its leaves, which contain ethereal oil and mucilage cells, gumbo filé, a powder used to give flavor and consistency to gumbo soup, is prepared.

Karen S. Velmure, whose original illustrations were used on the two preceding covers, also planned and executed this one, as well as the designs and devices in other parts of the Journal and on the offprint covers.

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THE GENERA OF CAESALPINIOIDEAE (LEGUMINOSAE) IN THE SOUTHEASTERN UNITED STATES [1]

KENNETH R. ROBERTSON AND YIN-TSE LEE

Subfamily CAESALPINIOIDEAE A. P. de Candolle, Prodromus 2: *tab.* inter 94 & 95, 473. 1825, "Caesalpinieae"
(CAESALPINIA SUBFAMILY)

Trees, shrubs, perennial or annual herbs, or (infrequently) lianas; in tribe Caesalpinieae plants often armed. Leaves alternate, persistent or deciduous, compound, even- [or odd-]pinnate or bipinnate, rarely ap-

[1] Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant BMS74–21469, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants in this area, with additional information from extraterritorial taxa in brackets. References that we have not seen are marked by an asterisk.

The treatments of *Gymnocladus* and *Gleditsia* are largely by Y. T. Lee, who prepared them while he was a Mercer Fellow of the Arnold Arboretum. The subfamily discussion and the treatments of the remaining genera are by K. R. Robertson. For the treatment of subfamily Mimosoideae, see T. S. Elias, Jour. Arnold Arb. **55:** 67–118. 1974.

Both plates of *Caesalpinia* and that of *Gymnocladus* were drawn by Karen S. Velmure; the plates of *Cercis* and *Cassia* are by Arnold D. Clapman; figures *a* and *e* of the *Gleditsia* illustration are by Sue Sargent, with the remaining figures by Arnold D. Clapman. Living and/or alcohol-preserved materials for these illustrations were collected by D. F. Austin, G. R. Cooley, T. S. Elias, W. T. Gillis, F. Harper, R. A. Howard, Y. T. Lee, K. R. Robertson, and C. E. Wood, Jr.

Professor Wood has freely given his critique and has continued to share his enormous knowledge of plants; his assistance is sincerely appreciated. Kathleen Clagett has given much editorial advice. Dr. Annetta Carter, University of California, Berkeley, kindly reviewed the treatment of *Parkinsonia* and has given permission to quote from her recent article on *Cercidium*. Considerable assistance has been given by R. M. Parkhurst, Stanford Research Institute, Menlo Park, California, on the saponin chemistry of *Gymnocladus* and *Gleditsia*. The manuscript was typed by Beverly Vincent.

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pearing simple [or unifoliolate or absent], petiolate; foliar glands on petiole or rachis present only in *Cassia*; pinnae and leaflets opposite or infrequently alternate; leaflets large to small, few to numerous or reduced and the rachis phyllodial, usually with entire margins, sometimes with pellucid dots; petioles, pinnae, and leaflets usually with a basal pulvinus; stipules paired, small to foliose or spinescent, caducous or persistent; stipels absent or rarely present and minute. Inflorescences terminal and/or axillary racemes, panicles, or spikes, sometimes reduced to subumbels or fascicles or the flowers solitary, sometimes cauliflorous; pedicels occasionally jointed; bracts usually present, small to conspicuous [or sepaloid], caducous to persistent. Flowers large to moderately small, often showy, usually bilaterally symmetrical, not papilionaceous (except in *Cercis*), yellow to pink, red, or purple, rarely or never blue, usually 5-merous except for gynoecium, perfect (or rarely imperfect in tribe Caesalpinieae and the plants then polygamous to dioecious). Sepals usually imbricate in aestivation, rarely valvate, the adaxial one sometimes cucullate, ± connate below into a short to long cup or tube [or free], sometimes also adnate to the receptacle and bases of the filaments and petals, forming a short to long floral cup or tube, the calyx lobes small to petaloid, ± equal to strongly unequal [rarely the entire calyx connate in bud and splitting irregularly as the flower opens]. Petals ascending-imbricate in bud, with the adaxial petal innermost and covered by the lateral ones, usually 5 [sometimes reduced to 4 or 1 or absent], free [or connate below], ± equal to strongly unequal, one petal often different from the others. Androecium usually bilaterally symmetrical and composed of 10 mostly unequal stamens in 2 whorls, rarely fewer [or numerous], all fertile or some reduced to staminodia; filaments short to greatly elongated, free to base or partly united [rarely diadelphous], often curving toward center of flower, usually pubescent at base; anthers dehiscing by longitudinal slits or apical [or basal] pores or slits, basifixed to dorsifixed, often versatile, lacking apical glands; pollen grains usually shed singly. Gynoecium of one sessile or stipitate carpel (except in abnormal flowers) inserted at base of floral or calyx cup or the gynophore adnate to the floral tube; ovary superior; style short to elongate, often curving adaxially; stigmatic area terminal, rarely oblique, small to dilated [or petaloid]; ovules anatropous, parietal, few to numerous in 2 rows on either side of the adaxial suture. Fruits very variable, stipitate or not, usually elongate [rarely globose], cylindrical to laterally compressed or flattened, straight or curved, sometimes winged, indehiscent, irregularly dehiscent, or dehiscent (sometimes elastically) along one or both sutures; externally constricted or not [or lomentlike], internally septate or not, with or without pulp; fruit walls chartaceous to woody or fleshy, glabrous to pubescent or echinate. Seeds large to rather small, ± globose to ovoid, rhomboid, or variously flattened, oriented transversely, obliquely, or longitudinally in the fruit, the hilum apical or subapical, small; seed coat usually very hard, variously marked, a closed pleurogram present in a few genera, but U-shaped pleurograms absent (cf. Mimosoideae); funiculus usually rather long; endosperm

abundant to lacking; embryo usually large, with large, flat cotyledons; radicle superior, short, thick, straight.

The Caesalpinioideae, one of three generally recognized subfamilies of Leguminosae (Fabaceae), includes 120 to 180 genera and 1500 to 3000 species, mostly of the tropics and subtropics. The subfamily is most diverse in both wet and dry areas of tropical America and tropical Africa, although few genera occur in both hemispheres. A smaller number of genera occur in tropical Asia, with relatively few genera in Polynesia, Australia, and the temperate regions of North and South America and Eurasia. Only a few genera (including *Cercis*, *Gymnocladus*, *Gleditsia*, and *Ceratonia* L.) are largely confined to temperate regions. Most genera of the subfamily are small, and, of the 152 genera (not including those of tribe Swartzieae) accepted by Hutchinson in his relatively conservative account (in which *Bauhinia* L., *Cassia*, and *Caesalpinia* are interpreted broadly), 62 are monotypic and 38 have from two to five species. In the broad sense, *Cassia* and *Bauhinia* are by far the largest genera, with about 600 and 570 species respectively; few, if any, of the other genera have more than 100 species.

There is general agreement that the three subfamilies that comprise the family Leguminosae, the Mimosoideae, Caesalpinioideae, and Faboideae,[2] are natural assemblages. There are differences of opinion, however, concerning the rank to be assigned to these taxa. Takhtajan and Hutchinson treat each as a family, i.e., the Mimosaceae, Caesalpiniaceae, and Fabaceae, of the order Fabales or Leguminales. Hutchinson (1964, p. 223) has said that "it is merely a matter of opinion or convenience (or even of prejudice!) whether Caesalpiniaceae should be treated as a separate family from Mimosaceae and Fabaceae (Papilionaceae) or all three regarded as subfamilies of Leguminosae." However, the distinguishing characters of the three taxa break down to such a degree that it seems far better to keep them at the rank of subfamily.

The subfamilial classification often used today follows that established by Bentham, with some modifications; see Heywood in Harborne *et al.* for a discussion of the classification of the subfamily and a very useful enumeration of the genera of Caesalpinioideae arranged alphabetically by tribes. The eight tribes of Caesalpinioideae usually recognized are Dimorphandreae Bentham (9 genera), Caesalpinieae Endl. (28 genera), Cassieae Bronn (20 genera), Detarieae DC. (Cynometreae Bentham emend. J. Léonard, 52 genera), Amherstieae Bentham emend. J. Léonard (33 genera), Cercideae Bronn (Bauhinieae Bentham, 11 genera; *Bauhinia* sensu lato, divided into 10 genera), Sclerolobieae Bentham (12 genera),

[2] The names Lotoideae and Papilionoideae have also been used for this subfamily. According to Article 19 of the *International Code of Botanical Nomenclature* (1969), the name of a subfamily that includes the type genus of a family must be based on the name of that genus. Since *Faba* Miller (= *Vicia* L.) is the type genus of the Leguminosae, the correct name for this subfamily is Faboideae. The name Papilionoideae cannot be used under any circumstance.

and Swartzieae DC. (11 genera) (sequence that of Brenan, 1967; number of genera from Heywood in Harborne *et al.*). *Amphimas* Pierre ex Harms (four species of tropical West Africa) was placed by Bentham in tribe Cadieae of subfam. Faboideae, but has been included by Schulze-Menz in the Caesalpinioideae as the sole genus of tribe Amphimanteae Pellegrin. Hutchinson considers the differences between Bentham's tribes to be slight and divides his family Caesalpiniaceae into two subfamilies, the Brachystegioideae (largely equivalent to tribe Amherstieae as emended by Léonard), with the calyx reduced and functionally replaced by sepaloid bracteoles, and the Caesalpinioideae, which was subdivided into five artificial groups. The systematic disposition of *Swartzia* and related genera is debatable. They have been considered to compose a tribe of subfam. Faboideae (Bentham) or of family Fabaceae (Hutchinson), a tribe of subfam. Caesalpinioideae (Taubert, Airy Shaw in Willis, Schulze-Menz, Brenan), or a distinct subfamily (De Candolle, Corner). *Krameria* L., sometimes assigned to the Caesalpinioideae, seems better placed in its own family (see K. R. Robertson).

Tribe Dimorphandreae (flowers small, mostly regular; stamens 10, in two whorls of alternating lengths, but usually otherwise uniform) approaches tribe Parkieae of subfam. Mimosoideae, and tribe Swartzieae (flowers nearly regular to irregular; calyx completely synsepalous in bud, splitting irregularly as the flowers open; embryo with a straight or curved radicle) is close to tribes Cadieae and Sophoreae of subfam. Faboideae.

In traditional systems of classification of Leguminosae, the sequence of the subfamilies, reflecting increasing morphological complexity, is (1) Mimosoideae, (2) Caesalpinioideae, and (3) Faboideae. Today, however, most phylogenists agree that the subfamily Caesalpinioideae is the least specialized and that it is linked through tribe Dimorphandreae to the Mimosoideae and through tribe Swartzieae to the Faboideae. Turner & Fearing proposed a hypothetical phyletic chart of the Caesalpinioideae and Faboideae based mainly on chromosome numbers. The tribes of Caesalpinioideae were considered to comprise three basic stocks: Amherstieae, in part ($x = 12, 14$), and "Eucaesalpinieae" ($x = 12, 14$); Bauhinieae ($x = 7$) and Cassieae ($x = 7$, with $x = 8$ secondary in *Cassia*); and Amherstieae, in part ($x = 8$), Cynometreae, in part ($x = 8, 10$), Sclerolobieae ($x = 11$), and Swartzieae ($x = 8$). According to Turner & Fearing, the Faboideae may be polyphyletic in origin from the last group of caesalpinioid tribes. Leguminosae, Chrysobalanaceae, and Rosaceae are sometimes included within the same order, and Hutchinson regards the caesalpinioid genera *Bandeiraea* Welw. ex Bentham & Hooker and *Bauhinia* to be connecting links between his Caesalpiniaceae and his tribe Chrysobalaneae of the Rosaceae (often separated as Chrysobalanaceae; see Prance, Jour. Arnold Arb. **51**: 522. 1970). Takhtajan says that his order Fabales (= Leguminosae in this paper) is "close to the Saxifragales and evidently derived from their immediate ancestor."

Like most primarily tropical and subtropical plant groups, the subfamily Caesalpinioideae is not very well known cytologically. Reported

sporophytic chromosome numbers (arranged by tribes) are Dimorphandreae, 24, 28; Caesalpinieae, 22, 24, 26, 28; Cassieae, 14, 16, 20, 22, 24, 26, 28, 32, 48, 56, 64; Detarieae (Cynometreae), 12, 16, 20, 22, 24, 36, 48; Amherstieae, 24, 28; Cercideae, 14, 28, 42; Sclerolobieae, 22; Amphimanteae, 22; and Swartzieae, 16, 20 (data mostly from Heywood in Harborne *et al.*). Most genera and species counted thus far have derived, polyploid base chromosome numbers of 12, 13, or 14. Very few species are reported as diploid, with base numbers of 6 (*Sindora siamensis* Teysm. ex Miq.), 7 (*Cercis canadensis*, *C. occidentalis*, *C. Siliquastrum*, *Cassia* sect. CHAMAECRISTA subsect. XEROCALYX), and 8 (*Sindora Supa* Merrill, *Trachylobium verrucosum* Oliver, *Swartzia madagascariensis* Desv., *Cassia* sect. CHAMAECRISTA subsect. LEIOCALYX). A base number of 8 has been reported in four tribes, although it is never common. Turner & Fearing postulate that "in view of the distribution of the $2n = 16$ diploid species in the family, particularly in the Caesalpinioideae, it seems most likely that 8 represents the original basal number for the Leguminosae, if such numerical archetypes exist. At a very early time, derived aneuploid lines of $x = 7$ might have given rise to the Bauhinieae and perhaps other $x = 14$ groups in the Caesalpinioideae as well as derived secondary aneuploids at the higher level of $x = 12$ and 13, but the major flow of the $x = 8$ line appears to have gone into the production of the Papilionoideae proper." The occurrence of somatic polyploid or aneuploid variant nuclei in root tip tissue has been noted in numerous genera of Caesalpinioideae and Mimosoideae, but not in genera of Faboideae (see Berger *et al.*, Sharma & Raju, and Turner & Fearing).

The pollen grains of most Caesalpinioideae are shed singly (Erdtman reports that the pollen of *Afzelia africana* Pers. remains in tetrads) and are nearly always 3-colporate (rarely appearing 3-porate), with narrow to broad, sometimes equatorially constricted, mostly elongate colpi and circular, lalongate, or infrequently lolongate ora. The shape of the grains in equatorial view is spheroidal, prolate, or oblate (infrequently flattened equatorially) and in polar view circular, 3-angled, or triangular. The exine is quite variable, both within and between genera, and may be smooth, punctate, rugulose, striate, reticulate, or verrucose. Considering the diversity of exine patterns in the species studied thus far, it would seem that a comprehensive survey of the subfamily with the use of the scanning electron microscope would be worthwhile, particularly for the larger genera.

Very little biological information about the genera of Caesalpinioideae is available, but the extraordinary diversity of flower and fruit structure indicates an equal diversity in the reproductive biology. There are few published accounts of pollinators of the Caesalpinioideae, but it seems that most species are pollinated by various diurnal insects. Some species of *Bauhinia*, *Eperua* Aublet, and *Hymenaea* L. are bat pollinated, and species of *Hardwickia* Roxb. are reportedly wind pollinated. Large black ants, hummingbirds, and bats visit the flowers of *Eperua rubiginosa* Miq., although it is not known what role each of these animals plays in the

actual pollination of this species (see Cowan, p. 15). Numerous floral modifications presumably linked to pollination occur in the subfamily, suggesting that detailed studies of floral biology would be worthwhile. (*Bauhinia* is particularly variable in this respect.)

The gynoecium of virtually all Caesalpinioideae consists of a single carpel that, by and large, is not too different in the various tribes and genera. Yet the diversity of fruit types in the subfamily is remarkable. Because of this variety (see subfamily description), the term "legume" is probably defined best as the fruit of members of the Leguminosae, although it is usually defined as a dry unicarpellate fruit that dehisces along both sutures.

Concomitant with the diverse morphology of the fruits are a number of dispersal mechanisms. Some selected examples follow. (The inclusion of a genus in one category does not necessarily imply that all species of that genus have the same mode of dispersal.) The fleshy or pulpy fruits of species of *Cassia*, *Ceratonia*, *Detarium* Juss., *Dialium* L., *Gleditsia*, *Gymnocladus*, *Hymenaea*, and *Tamarindus* are dispersed mostly by bats or arboreal or ground-dwelling mammals. Arils or arilloids are present in species of *Afzelia* Sm., *Copaifera* L., *Sindora* Miq., and *Swartzia* Schreber, and the seeds are largely dispersed by birds. Explosively dehiscent fruits are found in species of *Bauhinia*, *Brachystegia* Bentham, *Caesalpinia*, *Cassia*, *Delonix*, and *Eperua*. Winged or strongly flattened fruits dispersed by wind occur in species of *Burkea* Bentham, *Cercis*, *Daniellia* J. Benn. (endocarp winged), *Gleditsia*, and *Pterolobium* Wight & Arnott; in *Melanoxylon Brauna* Schott the seeds are winged. The fruits of *Gleditsia aquatica* and *Cynometra ramiflora* L. float and are transported by water; the seeds of *Caesalpinia* sect. GUILANDINA also float and are dispersed by ocean currents.

Subfamily Caesalpinioideae is of some economic importance, although it is not nearly as important as subfam. Faboideae. The fleshy fruits of *Tamarindus indicus*, tamarind, and *Ceratonia siliqua* L., locust bean, carob, or St. John's bread, are minor food crops in some parts of the world. A gum used in paper-making and in food products is obtained from the seeds of *C. siliqua*. Several species of *Cassia* yield the drug senna, and species of *Cassia*, *Caesalpinia*, and various other genera are used in folk remedies. Several species of *Caesalpinia* are important sources of tannin. The wood of numerous species of Caesalpinioideae is hard, heavy, and beautifully grained. Genera with commercially important wood include *Brachystegia*, zebrawood; *Caesalpinia*, types of Brazil wood; *Cassia*; *Copaifera*, purpleheart; *Guibourtia* J. Benn., bubinga; *Haematoxylon* L., logwood; *Hymenaea*, courbaril; *Macrolobium* Schreber, zebrawood; *Mora* Bentham; *Peltogyne* Vogel, purpleheart; *Peltophorum* (Vogel) Walp., canafistula; *Sindora*, supa; and *Swartzia*. Haematoxylin, used as a cytological stain and as a dye for wool, is obtained from the heartwood of *Haematoxylon campechianum* L.; brazil, a red dye, is extracted from the heartwood of several species of *Caesalpinia*; and sappan dye comes from *C. Sappan* L. Resins and copals are produced by species of *Copai-*

fera, *Cynometra* L., *Daniellia*, *Detarium*, *Gossweilerodendron* Harms, *Guibourtia*, and *Hymenaea*. Members of the Caesalpinioideae are often cultivated as ornamentals. Species of *Cercis*, *Gleditsia*, and, to a lesser degree, *Gymnocladus* are commonly seen in temperate regions, and species of *Amherstia* Wall.,[3] pride of Burma, *Bauhinia*, orchid tree, *Brownea* Jacquin, mountain rose, *Caesalpinia*, *Cassia*, *Colvillea* Bojer ex Hooker, *Delonix*, *Parkinsonia*, *Peltophorum*, and numerous other genera are cultivated in tropical and subtropical areas.

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[3] *Amherstia nobilis* Wall., sometimes called the most beautiful flowering tree in the world, rarely sets seed, is difficult to propagate from cuttings, and is sensitive to cool temperatures. Attempts to cultivate it in Florida have failed.

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KEY TO THE GENERA OF CAESALPINIOIDEAE IN THE SOUTHEASTERN UNITED STATES

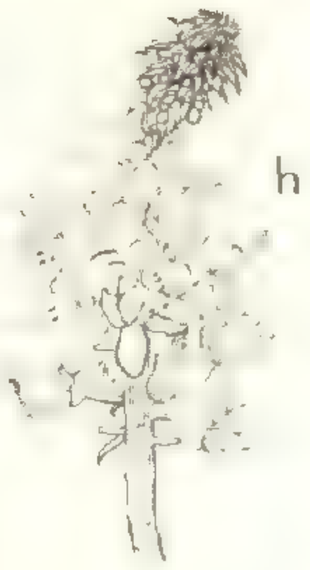
General characters: *trees or shrubs, rarely herbs; leaves mostly once pinnately compound, sometimes bipinnate, rarely appearing simple; rachises and leaflets with a basal pulvinus; stipels mostly absent; flowers mostly zygomorphic, papilionaceous only in* Cercis; *sepals imbricate; petals imbricate-ascending, with the upper petal innermost in bud; stamens 10 or fewer, mostly free; pollen grains shed singly; ovules anatropous; funiculus usually elongate; seeds without a U-shaped pleurogram (closed pleurograms present in some species of* Cassia *and a few other genera); hilum small, basal or subbasal.*

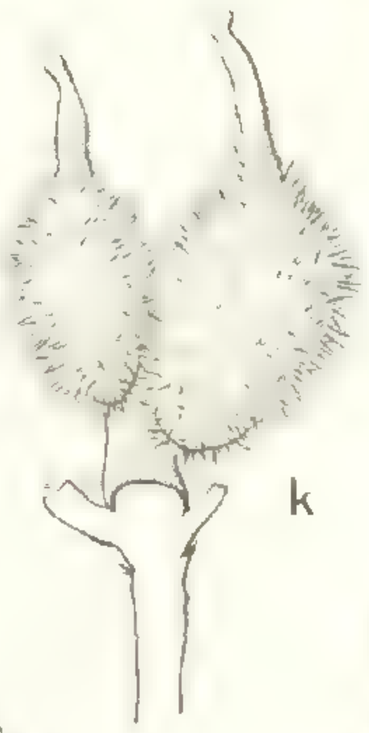
A. Leaves compound; flowers ± zygomorphic but not papilionaceous.
B. Leaves primarily twice pinnately compound, the primary pinnae phyllodial in *Parkinsonia*.
C. Leaves usually with several to many nonphyllodial pinnae and elongate petioles; leaflets small to large, not caducous; fruits various, usually not cylindrical-torulose; seeds arranged transversely.
D. Flowers zygomorphic (bilaterally symmetrical), yellow to red, perfect (or if imperfect, the plants scramblers); calyx lobes completely inclosing petals in bud; shrubs, trees, or scrambling vines.
E. Flowers small to moderately large, red and/or yellow; calyx lobes mostly imbricate in aestivation; fruits very variable, not strap-shaped with woody valves. ..... 1. *Caesalpinia*.
E. Flowers large, red to orange; calyx lobes ± valvate in aestivation; fruits very long, strap-shaped, dehiscent, the valves woody. ..... 2. *Delonix*.
D. Flowers ± actinomorphic (radially symmetrical), greenish, often imperfect; in bud petals visible between calyx lobes; deciduous trees.
F. Trees lacking thorns; leaflets broadly ovate, entire; flowers long-pedicellate, in open racemes or small panicles; fruits dehiscent along the placental suture, the valves woody. ..... 3. *Gymnocladus*.
F. Trees armed with thorns; leaflets narrowly ovate with crenate margins; flowers short-pedicellate, in short racemes; fruits strongly flattened, indehiscent or tardily dehiscent, the valves chartaceous. ..... 4. *Gleditsia*.
C. Leaves usually with 2 elongate, flattened, phyllodial pinnae on a very short axis that ends in a spine; leaflets small, numerous along margins of pinnae, caducous; fruits cylindrical-torulose; seeds arranged longitudinally. ..... 5. *Parkinsonia*.
B. Leaves once pinnately compound, without phyllodial pinnae.
G. Fertile stamens 4–10, filaments free; anthers usually basifixed, opening by terminal pores; petals ± equal or 1 or 2 somewhat smaller than the others; fruits varied, but not brown and fleshy with a crustaceous outer layer. ..... 6. *Cassia*.
G. Fertile stamens 2, staminal and staminodial filaments connate for half their length into a sheath open on the adaxial side; anthers dorsifixed, dehiscing by longitudinal slits; petals very unequal, upper 3 large, lower 2 minute, scalelike; fruit large, brown, ± sausage-shaped, fleshy, with a crustaceous outer layer. ..... 7. *Tamarindus*.
A. Leaves appearing simple, cordate; flowers papilionaceous. 8. *Cercis*.

Tribe CAESALPINIEAE Endl.

1. **Caesalpinia** Linnaeus, Sp. Pl. 1: 380. 1753; Gen. Pl. ed. 5. 178. 1754, "*Caesalpina*."

Shrubs, small trees, or scramblers, usually armed with recurved prickles. Leaves evenly [or oddly] twice pinnate, usually petiolate; rachises unarmed or with prickles; pinnae and leaflets several to many, opposite [or alternate], jointed basally; leaflets entire, eglandular [or with glands], the bases usually oblique; stipules absent or minute to conspicuously





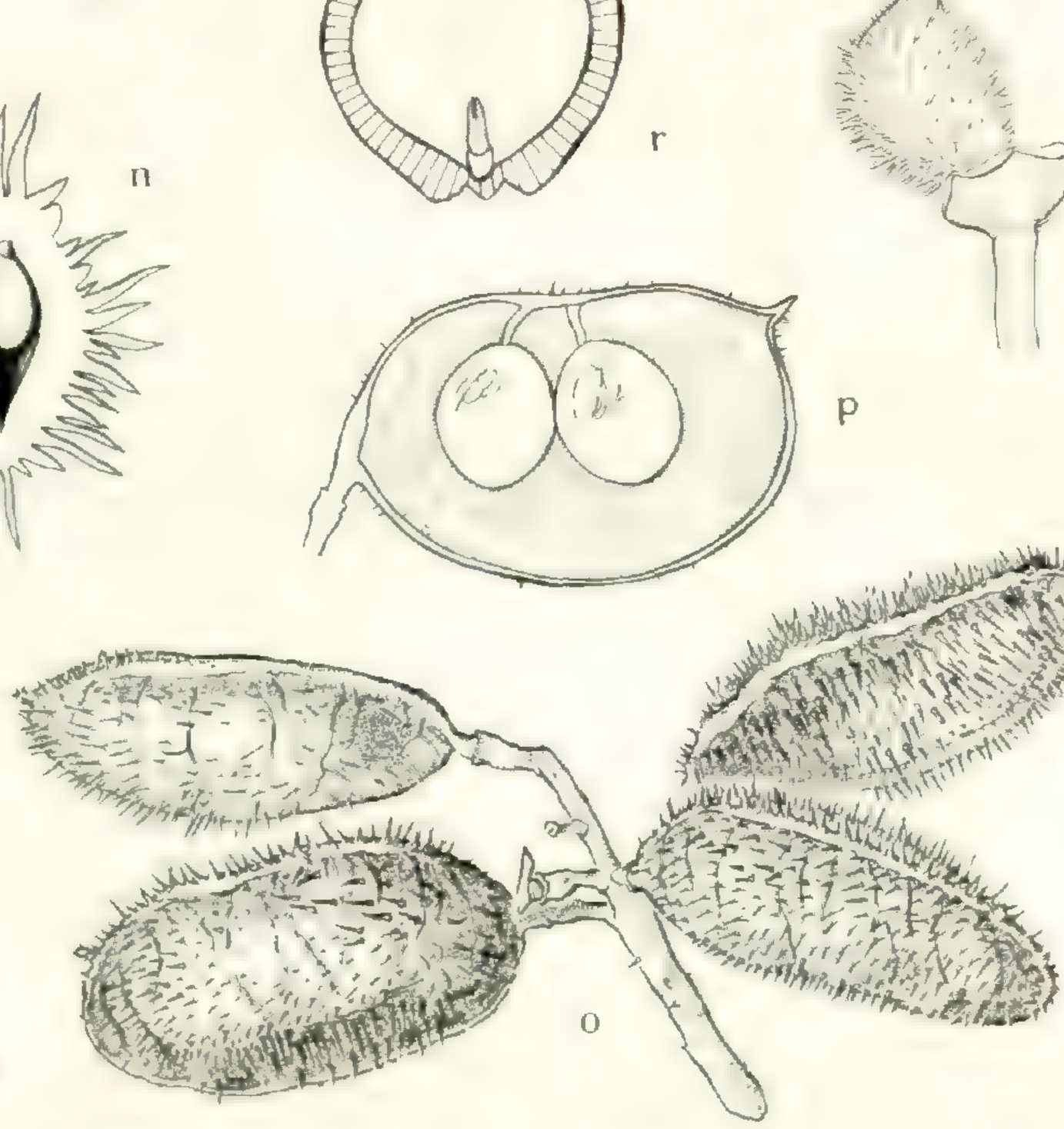


FIGURE 1. **Caesalpinia** section **Guilandina.** a–r, *C. Bonduc*: a, node with leaf, large persistent stipules, and axes of staminate inflorescences — note hooked prickles along rachis of leaf, × ¼; b, tip of staminate inflorescence, the bracts persistent until anthesis, × ½; c, bud of staminate flower showing cucullate lower calyx lobe, × 2; d, front view of staminate flower, × 2; e, same in side view, × 2; f, same in longitudinal section — note short floral cup and rudimentary gynoecium, × 3; g, rudimentary gynoecium from staminate flower, × 12; h, carpellate inflorescence, × ½; i, carpellate flower in longitudinal section showing the fertile carpel and well developed stamens lacking pollen,

leafy; stipels usually absent. Inflorescences several- to many-flowered, terminal or terminal and axillary [or falsely lateral] racemes or panicles, rarely reduced to solitary flowers; bracts usually caducous, sometimes persistent through anthesis; pedicels often jointed at base and near apex. Flowers perfect or imperfect in sect. GUILANDINA, the plants then dioecious. Calyx lobes 5, imbricate to almost valvate, nearly equal, the lower one sometimes cucullate and inclosing the others in bud, often same color as petals; calyx cup short [rarely campanulate]. Petals yellow and/or red, subequal and ± sessile except for the keel petal with its tubular claw and small blade. Stamens 10, all fertile (in perfect and staminate flowers); filaments of 2 lengths, free, glandular-pubescent below; anthers dorsifixed, versatile, opening by longitudinal slits. Gynoecium free of calyx cup; ovary subsessile or shortly stipitate, glabrous, pubescent, glandular, or echinate; ovules 2–10; style elongate, usually equaling or exceeding anthers; stigmatic area usually in a small funnel-shaped depression at tip of style, sometimes fringed. Fruits very variable, usually flattened or compressed, wings absent [or present], dehiscent or not, with or without septae, the pericarp hard and woody or leathery to chartaceous, glabrous, glandular, or echinate. Endosperm usually absent. (Including *Guilandina* L. and *Poinciana* L.) LECTOTYPE SPECIES: *C. brasiliensis* L.: see I. Urban, Symb. Antill. 2: 280. 1900[4]; see also N. L. Britton & P. Wilson, Sci. Surv. Porto Rico Virgin Is. 5: 377. 1924. (Name in commemoration of Andrea Cesalpino, 1519–1603, Italian physician and botanical observer.)

A diverse group of the tropics and subtropics of both hemispheres and particularly abundant in drier areas of southwestern North America, Central America, and South America. Estimates of the number of species to be recognized if the genus is interpreted broadly range from 60 to 280 (Hattink says ca. 100). The genus is subdivided either into a series of sections (or subgenera), as was done by De Candolle and Bentham & Hooker, or into a number of segregate genera. Britton & Rose recognized 14 such genera in North America. Since the problem of generic delimitation can be solved only by critically examining the group on a worldwide basis, *Caesalpinia* is conservatively treated here in the inclusive sense. The genus has been studied mostly in regional floras and is badly in need of a major taxonomic review.

× 3; j, carpel shortly after anthesis, calyx lobes removed, × 2; k, gynoecium from aberrant flower with 2 carpels, × 2; l, front view of stigma showing trichomes surrounding stigmatic cavity, × 12; m, tip of style in section to show stigmatic cavity, × 12; n, cross section of ovary, one ovule visible, × 5; o, mature infructescence with indehiscent, echinate fruits, × ½; p, slightly oblique section of nearly mature fruit showing 2 seeds, × ½; q, mature seed with finely cracked seed coat, × ½; r, soaked seed in vertical section, seed coat hatched, × 1.

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[4] According to Urban (p. 286), three elements were included by Linnaeus in this species: Plumier's plant, which is the type of the genus; *Peltophorum brasiliense* (Sw.) Urban (= *Caesalpinia violacea* (Miller) Standley); and *Caesalpinia bahamensis* Lam.

Caesalpinia Bonduc (L.) Roxb. (*C. crista* of authors, not of Linnaeus, 1753, as typified by Dandy & Exell; *Guilandina Bonduc* L.; *G. bonducella* L., 1762; *C. bonducella* (L.) Fleming), gray nicker bean, is widespread, mostly as part of the coastal strand vegetation, in the tropics and subtropics of both the eastern and western hemispheres. In Florida, it occurs mostly along the coastal sand dunes and hammocks, at least from Palm Beach on the eastern shore southward to Key West, north along the western shore to St. Petersburg, and on offshore islands to Levy County. *Caesalpinia Bonduc* is distinguished by large leaflets with acute to acuminate apices, conspicuous, foliaceous stipules, an armature of stout prickles and thin, straight bristles, and warm-gray seeds. *Caesalpinia major* (Medicus) Dandy & Exell (*C. Bonduc* of authors, not of Linnaeus, 1753, as typified by Dandy & Exell), yellow nicker bean, with inconspicuous or no stipules, an armature of prickles only, and yellowish seeds, is also widespread in both hemispheres, but it is not as common as *C. Bonduc*. Small, Britton & Rose, and Long & Lakela attribute this species (as *C. Bonduc*) to southern Florida, but no specimens that can definitely be assigned to this species have been seen by the present authors. *Caesalpinia ovalifolia* Urban (leaflets small, elliptical to suborbicular, with rounded to emarginate apices; seeds spherical, yellowish) was also reported from southern Florida by Small and Britton & Rose, but again there seem to be no specimens from our area. This species belongs to a group largely restricted to the West Indies; the taxonomy of the complex is unsettled.

Caesalpinia Bonduc, *C. major*, and *C. ovalifolia* belong to sect. GUILANDINA (L.) Bentham & Hooker (*Caesalpinia* subg. *Guilandina* (L.) J. G. Baker in J. D. Hooker), a very distinct group of perhaps 18 or fewer species mostly of coastal strands in the New World. Species of sect. GUILANDINA are trailing or scrambling shrubs with the stems and leaf rachises armed with recurved prickles (rarely unarmed); the flowers are imperfect and the plants dioecious; the staminate inflorescences are bracteate during anthesis; the fruits are usually echinate (rarely smooth), elliptical or oval, laterally compressed, few-seeded, and nonseptate, with rigidly chartaceous valves that dehisce completely along the placental suture and apically along the abaxial suture; and the seeds are rather large, hard, globose to ovoid, slightly flattened or not, and usually colored gray, yellow, orange-brown, or black. The seeds float in seawater and may be transported long distances by ocean currents (see Gunn and Ridley).

Caesalpinia pauciflora (Griseb.) C. Wright, of sect. CAESALPINIA, occurs in pinelands on the northern part of Big Pine Key, Monroe County, Florida, that is underlaid by Miami oölitic limestone; it also occurs in Cuba and Hispaniola. This species is a small shrub (becoming a small tree in Cuba) with two prickles at each node; numerous small, ovate or elliptic leaflets; small, yellow, perfect flowers with petals and stamens that more or less equal the calyx lobes (the flowers evidently do not open very widely, at least in Florida); and small, smooth, flat, elongate,

FIGURE 2. **Caesalpinia** sections **Caesalpinia** (a–j) and **Caesalpinaria** (k, l). a–j, *C. pauciflora*: a, tip of branch with bipinnately compound leaf and inflorescence, × ½; b, one pinna of leaf — note small spines at base, × 2; c, side view of flower, calyx lobes and one wing and one keel petal removed, × 3; d, "exploded" view of flower, × 3; e, lower stamen, × 5; f, gynoecium, × 5; g, off-center vertical section of ovary showing parietal ovules in 2 rows, × 12; h, fruit before dehiscence, × 1; i, seed and funiculus, × 3; j, embryo, × 3. k, l, *C. pulcherrima*: k, flower — note clawed banner petal, × 2; l, fruit, one valve removed, × ½.

nonseptate fruits that dehisce completely along both sutures, the valves then becoming twisted.

The taxonomy of sect. CAESALPINIA is problematical, and it is not clear how many species belong to it. The type species of the genus, *Caesalpinia brasiliensis*, is a very poorly known species endemic to Haiti. Linnaeus's inclusion of three elements in this species (see footnote 4) has caused considerable confusion. Urban (p. 280) effectively lectotypified the species by the plate in Plumier. Plants related to *C. brasiliensis*, in addition to *C. pauciflora*, include about a dozen described species of the Greater Antilles and the Bahama Islands and *C. sessilifolia* S. Watson, of Durango and Coahuila, Mexico. *Caesalpinia brasiliensis* (as *C. Crista* L.) was included in sect. SAPPANIA DC. by De Candolle and by Taubert in Engler & Prantl.

Caesalpinia pulcherrima (L.) Sw. (*Poinciana pulcherrima* L.), pride of Barbados, of sect. CAESALPINARIA Bentham & Hooker, is a beautiful shrub or small tree that is widely cultivated and naturalized throughout the tropics and subtropics. In our area, it persists after cultivation and also reproduces from seed in southern Florida. Brenan suggests that this species is a native of tropical America; others attribute it originally to tropical Asia. The rather large flowers are in elongate terminal racemes (some also axillary). The pedicels are several times the length of the petals, and the stamens are greatly exserted. When the flowers first open, the keel and wing petals are red with yellow margins, and the small blade of the clawed banner petal is entirely yellow. Later, the yellow color disappears, and the flowers are then entirely red. The shade of red varies from bright red to scarlet or orange-red, and there are plants with flowers that are entirely and permanently yellow. The smooth, unarmed, laterally flattened fruits of *C. pulcherrima*, like those of sect. CAESALPINIA, dehisce completely along both sutures, with the valves then becoming twisted. One of the valves usually remains attached to the pedicel. There are several transversely arranged, obovate, compressed, dark brown seeds in each fruit; the seeds are separated from one another by well developed septae.

Other exotic species possibly naturalized in Florida include *Caesalpinia Gilliesii* (Wall. ex Hooker) Dietr., bird-of-paradise or paradise poinciana, a native of South America (see Vines); *C. Sappan* L., of India and Burma (*McFarlin 4212* (A), Winter Haven, Polk County, Florida); and *C. Crista*, as typified by Dandy & Exell (*Ticanto Nuga* (L.) Medic.). A number of other species are grown as ornamentals in our area.

The bark of a number of species of *Caesalpinia*, particularly *C. coriaria* (Jacquin) Willd., divi-divi, *C. digyna* Rottl., *C. spinosa* (Mol.) O. Ktze., tara, and *C. melanocarpa* Griseb., are rich in tannins and are used both locally and commercially in the tanning of leather. Dyes are obtained from the fruit, bark, and wood of several species. Beautiful hardwoods that come from species of *Caesalpinia* include pernambuco wood (a type of Brazil wood) from *C. echinata* Lam.; sappan wood (another kind of Brazil wood) from *C. Sappan* L.; partridge wood from *C. Granadillo*

Pittier; and a type of ironwood from *C. ferrea* Mart. Decocts of various plant parts from numerous species of *Caesalpinia* are used as herb remedies. The seeds of species of sect. GUILANDINA are made into jewelry. Several species, including *C. pulcherrima*, *C. Gilliesii*, and *C. decapetala* (Roth) Alston, are commonly cultivated in tropical and subtropical regions. The bark of *C. eriostachys* Bentham and the stems and pulp of the fruits of *C. Crista* (*C. Nuga* L.) are used to stupefy fish.

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2. **Delonix** Rafinesque, Fl. Telluriana 2: 92. 1836.

Small to medium-sized unarmed trees with broad, rounded crowns and arching branches, the crown spread greater than height of tree, deciduous for brief periods or evergreen; twigs pubescent, with prominent lenticels; trunks buttressed at base; bark gray-brown, smooth, with many lenticels. Leaves alternate, evenly twice pinnate, with 10–25 pairs of pinnae, fairly large, the petiole with a basal pulvinus; pinnae opposite, with 12–40 pairs of leaflets and a basal pulvinus; leaflets opposite, quite small, finely pubescent on both surfaces, rounded at base and apex, nearly sessile, with a pulvinus; stipules simply or incompletely twice pinnate [or simple and subulate], caducous. Inflorescences elongate, several-flowered racemes at tips of growth of the season, overtopping the leaves; pedicels long, stout, articulated at each end; bracts ovate, with tapering apices, caducous. Flowers very showy, large, scarlet or red to orange, perfect, appearing with or before the leaves. Calyx lobes 5, green on abaxial surface, red with yellow border on adaxial surface, equal, thick, free, spreading, half as long as the petals, valvate in aestivation; calyx cup very short. Petals 5, long-clawed, becoming reflexed with age, wing and keel petals ± equal, the banner petal larger. Androecium of 10 long-exserted stamens, all fertile; filaments slightly unequal in length, free to the base, curving adaxially, basally pubescent; anthers yellow and red, dorsifixed, versatile. Carpel shortly stipitate, inserted in center of small, nectiferous receptacle; ovary elongate, pubescent; style equaling or exceeding stamens, curving adaxially; stigma punctiform; ovules numerous. Fruits pendulous, septate, large (sometimes more than 0.6 m.), strap-shaped, straight or slightly scimitar-shaped, laterally compressed, woody, long-persistent, eventually opening along both sutures. Seeds numerous, sunken in transverse depressions in valves, narrowly [or broadly] ellipsoid, somewhat laterally flattened, red-brown, with lighter areas on each face; seed coat hard; embryo elongate, laterally flattened; endosperm present. Base chromosome number 24, 28. TYPE SPECIES: *Poinciana regia* Bojer ex W. J. Hooker = *D. regia* (Bojer ex W. J. Hooker) Raf. (Name derived from Greek *delos*, evident, and *onyx*, claw, in reference to the petals.)

A genus of three species, *Delonix regia* (a native of Madagascar, evidently rare in nature, widely cultivated throughout the tropics), *D. elata* (L.) Gambel (eastern Africa, southwestern Asia, India), and *D. Baccal* (Chiov.) Baker f. (eastern Africa). Capuron recently reduced *Aprevalia* Baillon to a section of *Delonix*, including in it seven species of Madagascar that had mostly been placed previously in *Aprevalia* or *Poinciana*.

Delonix regia, flamboyant, flamboyan, or royal poinciana, one of the most spectacular ornamental trees of the tropics, is commonly planted in southern Florida, and it is occasionally spontaneous in hammocks and pinelands. The trees are deciduous in areas where there is a distinct dry season, with the flowers appearing at the tips of the new growth of the

season on the seemingly bare trees. In our area, where rainfall is more uniform throughout the year, although the winters in Florida are dry, this species is mostly evergreen and the flowers overtop the leaves of the previous year. There are several color forms, with the overall color of the flower being scarlet, red, or orange. The calyx lobes are green on the abaxial surface and red (to orange, depending on the form) with yellow margins on the adaxial surface. The lateral and lower petals are red, with rather faint yellow streaks at the bases of the blades. The banner petal has red margins, with the central portion of the blade white with red streaks and the base of the claw bright yellow streaked with red. The banner petal evidently functions as a signal to pollinators, since it is fully expanded at anthesis, but the lateral margins soon roll inward and the white and yellow fade to red. This petal often falls from the flower before the wing and keel petals.

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3. **Gymnocladus** Lamarck, Encycl. Méth. Bot. 1: 733. 1785 ('1783').

Unarmed deciduous trees with narrow, rounded crowns; trunks forking into few, ascending main branches; branchlets stout, blunt, with a large pinkish pith; bark initially smooth, lenticellate, becoming very rough, with large plates attached along one side, and finally thick, with numerous, flat scales; axillary buds *2*, superposed, in pubescent depressions; terminal bud absent; leaf scars large, irregularly cordate [or V-shaped], with 3–5[–13] rather indefinite bundle scars. Leaves large, mostly evenly bipinnate, long-petiolate, the petiole with a basal pulvinus; pin-

nae many-foliolate, the lower 1 or 2 pairs often reduced to single leaflets; leaflets shortly petiolulate, ovate to elliptical, with acuminate apices, entire margins, and slightly oblique bases; stipules lanceolate, caducous; stipels absent [or minute, awl-shaped, persistent]. Inflorescences erect [or drooping] racemes or panicles terminating growth of the year and from buds on wood of last year, those composed of carpellate flowers more elongate and racemose than those composed of staminate flowers; bracts and bracteoles small, caducous. Flowers regular, strongly fragrant, perfect or imperfect, the plants dioecious to occasionally polygamous. Calyx lobes 5, subequal, lanceolate, with acute apices, equaling and the same color as the petals, valvate in aestivation, but incompletely inclosing the petals; floral tube narrowly campanulate, 10-ribbed, pubescent and dark reddish purple without, lined with nectariferous tissue. Petals 5 (rarely 4), greenish white, sometimes dark reddish purple on the abaxial surface, pubescent, narrowly oblong with obtuse or acutish apices, keeled, imbricate in aestivation, inserted around opening of floral tube. Stamens 10, in 2 whorls of 5; filaments alternately long and short, free to the base, inserted as the petals; anthers dorsifixed, bright yellow or orange, polliniferous in staminate flowers, without pollen in carpellate flowers. Carpel well developed in carpellate flowers, variously reduced or rudimentary in staminate flowers, sessile or shortly stipitate, many-ovulate, inserted at base of floral tube; style short, stout, erect, exserted beyond anthers in carpellate flowers; stigma oblique, dilated, bilobed [or capitate]. Fruits pendent, obliquely stalked, laterally compressed, variously ovate, ellipsoid, oblong, or ± falcate, 1–several-seeded, dehiscent along placental suture (but seeds retained in fruit), some persistent on trees through winter; valves dark reddish brown, glaucous or shiny, woody, smooth [or transversely ridged and grooved]; pulp surrounding seeds green, bitter, poisonous. Seeds large, compressed, broadly ovoid to obovoid or round, dark reddish brown, attached by a stout funiculus; seed coat thick, hard; embryo surrounded by a layer of cartilaginous endosperm. Germination hypogeal; juvenile leaves once pinnate. Base chromosome number 14. LECTOTYPE SPECIES: *G. canadensis* Lam. = *G. dioicus* (L.) Koch; typified by the removal of *G. arabica* Lam. to *Moringa* Adanson by Persoon, Syn. Pl. 1: 461. 1805; see also C. S. Sargent, Silva 3: 67. 1892. (Name derived from Greek *gymnos*, naked, and *klados*, a branch, alluding to the stout branches destitute of foliage for many months.[5]) — COFFEE-TREE.

A small genus of eastern North America and eastern Asia (the only genus of the Caesalpinioideae confined to these two regions), with *Gymnocladus dioicus* in eastern North America; *G. chinensis* Baillon in central

[5] The name *Gymnocladus* has been treated as either masculine or feminine. According to Article 75A(2) of the 1972 edition of the *International Code of Botanical Nomenclature*, "generic names formed from two or more Greek or Latin words should take the gender of the last . . . ." Since *klados*, transliterated into Latin as *cladus*, is masculine, it follows that *Gymnocladus* is also masculine.

and southeastern China; *G. assamicus* P. C. Kanjilal in Assam, India, and southeastern Yunnan, China; and *G. burmanicus* C. E. Parkinson in Lower Burma.

Gymnocladus dioicus, Kentucky coffee-tree, $2n = 28$, a tall tree with a few ascending branches and a narrow crown, stout twigs, and evenly bipinnate leaves that, considering their length, are among the largest of any tree in eastern North America, is native primarily to the west of the Appalachians from central New York to southeastern Ontario, Wisconsin, and southeastern South Dakota, southward to Kentucky, Tennessee, Arkansas, and Oklahoma; it is widely cultivated and has become naturalized to the north, south, and east of its original range. The species occurs mostly in low or rich woods as isolated trees or small colonies of widely separated individuals produced from root suckers sent up some distance from the parent tree; associated species include *Juglans nigra* (black walnut), *Acer saccharum* (sugar maple), *Tilia americana* (basswood), *Asimina triloba* (pawpaw), *Ulmus rubra* (slippery elm), *Fraxinus quadrangulata* (blue ash), *Populus deltoides* (cottonwood), and *Quercus rubra* and *Q. alba* (red and white oaks). Indians and early settlers sometimes planted *G. dioicus* near their dwellings, and the scattered distribution of the species is sometimes attributed to this practice. *Gymnocladus dioicus* is one of the last trees to expand its leaves in spring and the earliest to shed them in autumn, the leaflets turning yellow and falling from the rachis, which drops later.

The highly fragrant geraniol-scented flowers of *Gymnocladus dioicus* are moderately large, but they are greenish, not showy, and mostly radially symmetrical, with a long floral tube (containing abundant nectar). The petals and calyx lobes are about equal in length. The aestivation of the calyx is unusual in that it is incompletely valvate, with the lateral margins of the lobes not touching each other and the petals thus visible between them (FIGURE 3c). There are evidently two basic types of flower, each confined to different trees. Functionally staminate flowers, borne in compact panicles, have polliniferous anthers and a variously reduced but sterile gynoecium (FIGURE 3f, g). Morphologically perfect but mostly functionally carpellate flowers (the anthers lacking pollen) occur in elongate racemes or lax panicles (FIGURE 3b, h). Studies of the breeding system of *G. dioicus* in nature are lacking, but observations on several living trees cultivated in the Boston area and data from herbarium specimens indicate that this species is mostly dioecious, with some degree of polygamy. Two trees in the Arnold Arboretum that bear morphologically perfect flowers consistently set fruit, even though pollen appears to be lacking and there are no known staminate trees within a radius of several miles. The Asiatic species also appear to be predominantly dioecious.

The broad, elongate, somewhat compressed, reddish-brown fruits of *Gymnocladus dioicus* are retained on the tree after the leaves have fallen, with some remaining through winter. While the fruits are on the tree, or after they have fallen, the leathery-woody valves open slightly

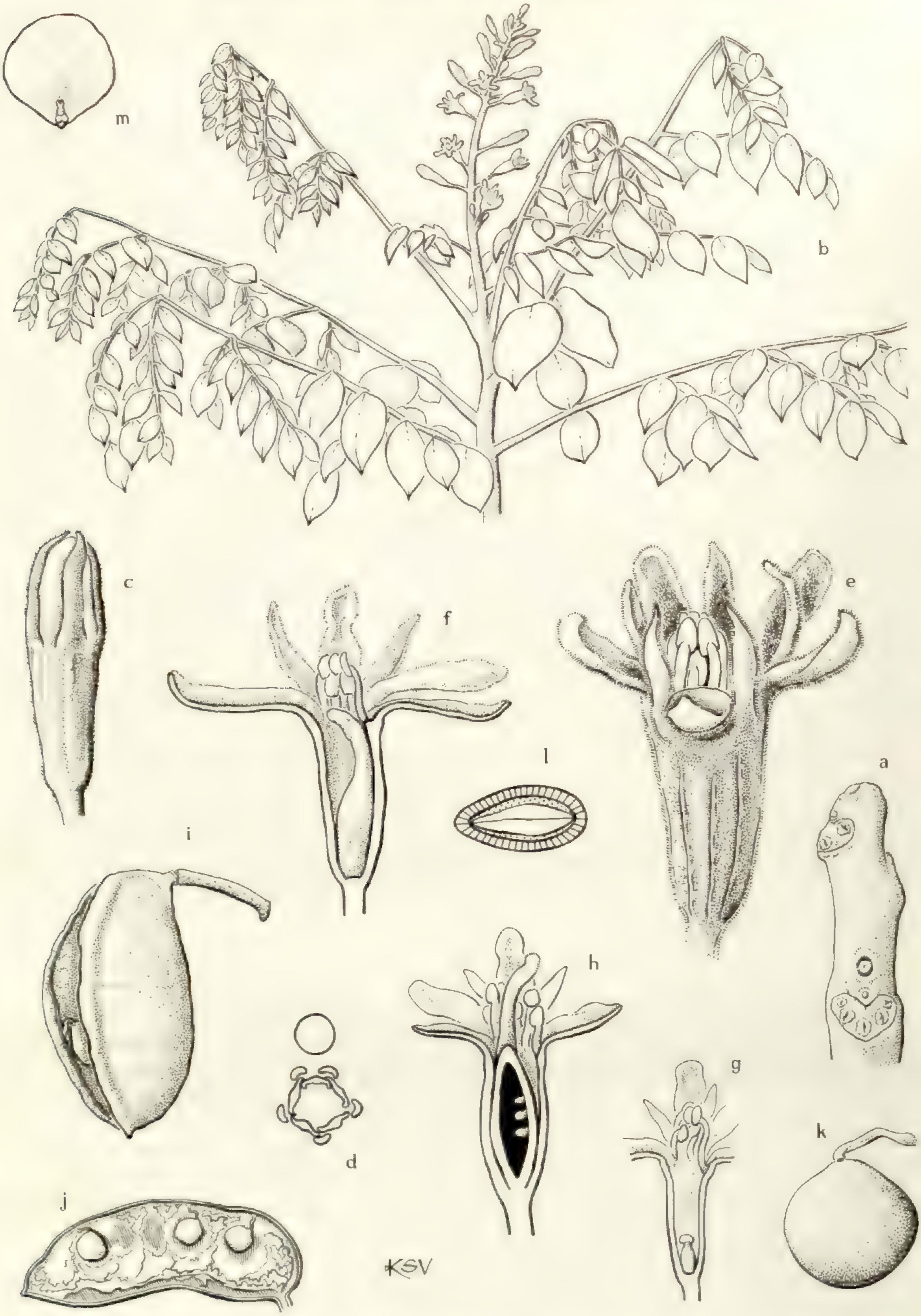

FIGURE 3. **Gymnocladus.** a–m, *G. dioicus*: a, winter twig, buds superposed, terminal bud absent, × 1; b, tip of flowering branch, leaves bipinnately compound, × ¼; c, flower bud, calyx lobes not completely covering petals, × 2; d, diagrammatic cross section of flower bud to show aestivation, androecium and gynoecium not shown, inflorescence axis represented by circle — note that adaxial petal is innermost, × 2; e, functionally staminate flower, × 3; f, same in vertical section to show relationship of stamens and sterile gynoecium, × 2;

along the placental suture, but the seeds are retained in the pod and are released only when the fruit is eaten by animals or when the valves decay. The seeds are surrounded by a green, sticky, bitter-tasting pulp. The large, compressed-globose seeds have a thick seed coat and may remain in the ground for many years before germinating.

About ten extinct species of *Gymnocladus*, mostly fossil leaf and fruit compressions, have been described from the central and western United States, Mexico, Europe, and China.

The fruits of *Gymnocladus* are rich in saponins, and those of *G. chinensis* and *G. assamicus* have been used for various washing purposes both in eastern China and among the Khasis in Assam, India. In a recent study of the chemical nature of the saponins and their sapogenins in *G. dioicus*, *G. chinensis*, and *G. assamicus* (Lee & Parkhurst, unpublished data), four major triterpenoid aglycones were found, with only minor quantitative differences between the species. The four compounds are different from, although structurally similar to, those found in species of *Gleditsia*. Saponin extracts from fruits of *G. chinensis* have blastocidal activity, and very low concentrations can terminate pregnancy in rats. This effect may be due to the cytotoxic action of the saponins on rapidly dividing embryonic cells (Parkhurst, pers. comm.).

The Pawnee and Meskwaki Indian tribes reportedly roasted the seeds of *Gymnocladus dioicus* like chestnuts for food, and early European settlers tried using the seeds as a coffee substitute. The wood of *G. dioicus* has been used locally for cabinet work and also for fence posts, since it is resistant to decay. This species is occasionally cultivated in parks and yards. People sometimes unwittingly plant this species, mistaking its seedlings for those of *Juglans nigra*, black walnut.

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g, portion of staminate flower with highly reduced gynoecium, × 2; h, functionally carpellate flower in vertical section, anthers without pollen, × 2; i, mature fruit dehiscing along adaxial (placental) suture, one seed visible, × ½; j, fruit, one valve removed, seeds surrounded by fleshy pulp (unshaded), × ¼; k, seed with long funiculus, × 1; l, cross section of seed, seed coat hatched, endosperm even-stippled, cotyledons unshaded, × 1; m, embryo, one cotyledon removed, × 1.

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4. **Gleditsia** Linnaeus, Sp. Pl. 2: 1056. 1753; Gen. Pl. ed. 5. 476. 1754.

Deciduous trees with open crowns [or shrubs]; trunks and branches usually armed with stout, simple or branched thorns; branches zigzagged, apically thickened; bark smooth, becoming lenticellate and eventually deeply fissured, with the ridges curved outward on one side; buds minute, several, superposed, the terminal bud absent; leaf scars irregularly U-shaped with 3 bundle traces. First leaves of the year (those preformed in buds of the previous year) evenly once pinnate, apparently fasciculate, the internodes short; later leaves evenly bipinnate with much longer internodes; leaflets small to medium-sized, numerous, subopposite to alternate, with crenate (rarely entire) margins and slightly oblique bases; stipules minute, caducous. Inflorescences axillary, solitary, or fascicled racemes [occasionally panicles] usually appearing with first leaves of the season; staminate inflorescences with numerous, congested flowers, the carpellate and perfect inflorescences lax, with fewer flowers; bracts scalelike, caducous. Flowers small, regular, perfect or imperfect, the plants polygamous to dioecious. Calyx lobes 3–5, subequal, colored like and as large as the petals, deciduous, valvate in aestivation, but incompletely inclosing petals; floral tube campanulate, lined with nectariferous tissue. Petals as many as the calyx lobes, subequal, not clawed, greenish to creamy white, inserted at margin of floral tube, imbricate in aestivation. Staminate flowers with 4–6[–10] exserted stamens; filaments filiform, free to base, pubescent below, inserted at apex of floral tube; anthers subequal, dorsifixed; gynoecium rudimentary or absent. Carpellate flowers with 4–6[–10] staminodia, the anthers small to aborted, lacking pollen; gynoecium sessile or very shortly stipitate, inserted at base of floral tube; style short, oblique; stigma prominent, dilated, bilobed, ± perpendicular to axis of flowers; ovules 2–many. Perfect flowers similar to carpellate ones, except some anthers polliniferous. Fruit stipitate, strongly flattened laterally [or merely compressed], broadly elliptical and one-seeded or elongate, many-seeded, and variously straight, falcate, undulate, or twisted; pericarp chartaceous [to woody], smooth or conspicuously veined, sometimes glaucous, indehiscent or tardily dehiscent; pulp present or absent. Seeds transverse in fruit, separated by membranaceous septae or not, broadly ellipsoid to subquadrate, compressed; seed coat light brown to greenish brown, thin; embryo surrounded by thick layer of cartilaginous endosperm. Germination epigeal, juvenile

leaves once pinnate. Base chromosome number 14. TYPE SPECIES: *G. triacanthos* L. (Name commemorating J. G. Gleditsch, 1714–1786, German botanist; spelling sometimes erroneously altered to *Gleditschia* or *Gleditzia*.) — HONEY LOCUST.

A small genus of about 14 species disjunct in four regions: two or three species in eastern North America; *Gleditsia amorphoides* (Griseb.) Taub. in northern Argentina and adjacent Uruguay, Paraguay, and Brazil; *G. caspica* Desf. in the area surrounding the Caspian Sea; *G. assamica* Bor, a very poorly known species from northeastern India; and eight species in Asia from eastern, central, and southwestern China to Korea, Japan, Vietnam, and the Philippine Islands. *G. africana* Bentham (Senegal to the Sudan Republic, south to Zambia, Rhodesia, and Southwest Africa) is now considered to be a species of *Erythrophleum* R. Br. (see Brenan, 1967, subfamily references).

Gleditsia triacanthos, honey locust, $2n = 28$, characterized by the indehiscent, elongate, many-seeded fruits with the seeds surrounded by a sweet pulp and separated by membranaceous septae, is a common tree of the midwestern United States, where it occurs in a variety of habitats, from moist woods along rivers and streams to dry or upland slopes and pastures. The natural distribution of this species is from western New York and extreme southwestern Ontario (introduced?) to southeastern South Dakota southward to eastern Texas and along the western edge of the Appalachian Mountains to northwestern Florida. *G. triacanthos* is widely cultivated and has become naturalized east of the Appalachians from South Carolina to New England and Nova Scotia and perhaps also to the west of its original range. *Gleditsia aquatica* Marsh. (*G. monosperma* Walt.), water locust, $2n = 28$, is largely ecologically and geographically isolated from *G. triacanthos*, occurring in swamps and low wet woods and along the borders of bayous and sloughs on the Coastal Plain from eastern South Carolina to central Florida and eastern Texas and northward in the Mississippi and Ohio River valleys to Missouri, Kentucky, Illinois, and Indiana. The fruits of *G. aquatica* are mostly one-seeded, short, tapering-elliptical in outline, strongly flattened, light in weight, without pulp, and tardily dehiscent.

Plants with fruits intermediate between those of *Gleditsia triacanthos* and *G. aquatica* were first discovered in Brazoria County, Texas, by Sargent, who named them *G. texana*; he later suggested that these intermediate forms might be of hybrid origin. Similar plants have since been found in scattered areas in Indiana, Arkansas, Mississippi, and Louisiana (evidently always in the area where the distributions of *G. triacanthos* and *G. aquatica* overlap). The taxonomic disposition of these plants differs, some authors placing them within the range of variation of *G. triacanthos* (see illustration on p. 533 of Vines, subfamily references, for variations that occur in Brazoria County, Texas), others recognizing them as a distinct species, *G. texana*, and still others considering them to be F_1 hybrids, *G.* × *texana* Sargent (pro. sp.).

Simple to complexly branched thorns, generally considered to be modified lateral branches, are found on the twigs, branches, and/or trunks of all species of *Gleditsia*. The abundance and size of the thorns vary greatly, both on the same individual and between individuals of the same species. In *G. triacanthos* the thorns decrease in frequency toward the

FIGURE 4. **Gleditsia.** a–j, *G. triacanthos*: a, tip of branch with staminate inflorescences — note once pinnately compound leaves on short shoots, × ½; b, staminate flower with 4 stamens, × 3; c, carpellate flower, × 3; d, same in vertical section — note perigynous insertion of calyx lobes, petals, and stamens and orientation of gynoecium, × 4; e, mature fruit, × ¼; f, seed, × 2; g, soaked seed in cross section, endosperm even-stippled, seed coat and cotyledons unshaded, × 1; h, embryo from soaked seed, × 1; i, thorn from branch, × ¼; j, thorn from tree trunk, × ¼.

top of the trees, and "thornless" trees may be produced by grafting buds taken from near the top of a tree onto normal rootstocks. Included in *G. triacanthos* f. *inermis* (L.) Zabel are the various "thornless" cultivars, but none of these plants are totally devoid of thorns.

Very little is known about the root systems of the species of *Gleditsia*. *Gleditsia triacanthos* produces a strong taproot and a profusely branched lateral root system that penetrates the soil to a depth of 10 to 20 feet. The root system of *G. aquatica* is apparently adapted to swampy conditions. No root nodules have been reported in *Gleditsia*.

The flowers are usually imperfect, but they are sometimes perfect. In *Gleditsia triacanthos* individual trees evidently may have only staminate flowers, carpellate/perfect flowers, or all three types of flowers. Branches of a tree tend to have only one type of flower. Since herbarium specimens are usually prepared from a single branch, only extensive field studies can ascertain the degree of polygamy or dioecism in this species. However, the situation in *G. triacanthos* and other species in the genus may be considered as an intermediate step toward complete dioecism.

The fruits of *Gleditsia* vary considerably from species to species. Two groups may be recognized, species with fruits that contain pulp and those in which it is lacking. Some of the pulp-containing fruits are woody and subcylindrical; others are chartaceous and strongly laterally compressed. The very light fruits of *G. aquatica* are probably dispersed primarily by wind and water. The fruits of *G. triacanthos* are larger and heavier, but they are still capable of being carried by wind and water. Moreover, the fruits and/or seeds of *G. triacanthos* are readily eaten by cattle, squirrels, rabbits, and rats, with some of the seeds passing intact through the animals' digestive tracts.

The fruits of *Gleditsia* are rich in saponins, and the pods of *G. sinensis* Lam., *G. japonica* Miq., and *G. fera* (Lour.) Merr. are used as soap substitutes in China, Japan, and Indochina. Preliminary analyses indicate that eight major triterpenoid sapogenins or aglycones are found in *G. triacanthos*, *G. sinensis*, and *G. officinalis* Hemsley, with oleanolic acid and echinocystic acid (identification tentative) being the predominant compounds (Parkhurst & Lee, unpublished data). Although final separation and identification of these compounds are pending, it is clear that all three species have the same set of sapogenins. It is noteworthy that *Gleditsia* evidently shares no major sapogenins with *Gymnocladus*.

A chromosome number of $2n = 28$ has been reported in *Gleditsia amorphoides*, *G. aquatica*, *G. fera* (southern China and Vietnam), *G. microphylla* Gordon ex Y. T. Lee [6] (central China), *G. japonica* (as *G. horrida* Willd., northeastern China, Korea, and Japan), *G. ? sinensis*, and *G. triacanthos*. Recent studies on Asiatic species of *Gleditsia* by Y. T. Lee indicate that both *G. sinensis* (eastern and central China) and *G. australis*

[6] **Gleditsia microphylla** Gordon ex Y. T. Lee, nom. nov. *G. heterophylla* Bunge, Mém. Acad. Sci. St. Pétersbourgh Savants Étr. 2: 29. 1833, not *G. heterophylla* Raf., Fl. Ludovic. 99. 1817. TYPE: China, in mountains near Lun-Zùan-ssy and Ssi-jui-ssy, *A. Bunge s.n.*, 1831 (K!).

Hemsley (southern China and Vietnam) share the same diploid number as the others.

Some 40 extinct *Gleditsia* or *Gleditsia*-like species have been reported in the literature. These fossils are mostly compressions of leaflets, thorns, fruits, or silicified wood; no microfossils have been found. Fossils of *Gleditsia* have been found in places outside the present range of the genus (e.g., Europe and western North America), indicating a much wider distribution of the genus in the past.

Gleditsia triacanthos is widely cultivated as an ornamental in the United States, especially in those areas where *Ulmus americana* has been seriously affected by the elm disease (*Ceratocystis ulmi*). It is also commonly cultivated in Europe and Asia (for names of cultivars see Wagenknecht, 1961).

The pulp around the seeds of *Gleditsia triacanthos* is sweet, and the pods are used as a trail food and an ingredient in folk beers. Wild animals and cattle readily eat the pods. The thorns on the trunks and branches of this species have been used as sewing needles, as tools for carding wool, and, when tied to sticks, as weapons by country people for hunting bullfrogs (Steyermark, Fl. Missouri, p. 873). The wood of *G. triacanthos* is very strong and durable and has been used for fence posts and railroad ties. The Cherokee Indians of Tennessee reportedly made bows from the wood of this plant. The wood of *G. aquatica* is also strong and durable. It is used for fence posts and has qualities that would make it a fine cabinet wood.

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5. **Parkinsonia** Linnaeus, Sp. Pl. 1: 375. 1753; Gen. Pl. ed. 5. 177. 1754.

Armed evergreen shrubs or small trees, branching near base, with broad, very open crowns; branches slender, often pendent, slightly zigzagged; bark thin, yellow-green, smooth, eventually becoming reddish brown and breaking into small flakes or plates; buds solitary or superposed. Leaves alternate, evenly twice pinnately compound, with 2, infrequently 4 or 6, opposite pinnae on a very short main axis that terminates in a spine (the whole leaf appearing as 2 or more simply pinnate leaves); rachis of pinnae elongate, flattened, narrow, persistent, and phyllodial; leaflets opposite to partly alternate, sessile, numerous, small, deciduous; stipules spinescent, persistent or caducous; axillary leaves lacking spines, sometimes produced in fascicles from axils of primary leaves. Inflorescences solitary or fascicled, slender, elongate, several-flowered racemes axillary on growth of the year, appearing with the leaves; pedicels slender, about as long as the diameter of the flowers, jointed just below them, subtended by a small, scalelike, caducous bract. Flowers perfect, moderate-sized, showy, fragrant. Calyx synsepalous, the lobes 5, equal, narrowly triangular, reflexed at anthesis, strongly imbricate in bud, deciduous; calyx cup shorter than lobes, obliquely campanulate, persistent. Petals 5, much longer than the calyx lobes, nearly equal, bright yellow fading to reddish, spreading, shortly clawed, slightly erose, the banner petal with conspicuous red spots and a longer, basally glandular claw. Androecium of 10 stamens in 2 series of 5, shorter than the petals; filaments free to the base, the one opposite banner petal enlarged at base, gibbous on abaxial side; anthers dorsifixed, versatile. Gynoecium shortly stipitate, pubescent when young; style slender, curving adaxially, equaling or slightly exceeding stamens; stigma minute; ovules numerous. Fruits pendent, cylindrical, constricted externally between and beyond the seeds (torulose), tapering at both ends, the wall rather thin, longitudinally striate, the exocarp separating in strips from the endocarp, supposedly tardily dehiscent by 2 valves. Seeds few, widely spaced, longitudinally arranged, oblong, slightly flattened, smooth, brown; seed coat thin; endosperm abundant on either side of embryo; embryo bright yellow, the cotyledons flattened, broadly ellipsoid, auriculate at base, the radicle short, broad, straight. Base chromosome number 7. TYPE SPECIES: *P. aculeata* L. (Name commemorating John Parkinson, 1567–1650, English florist, apothecary, herbalist, and author.) — JERUSALEM-THORN.

One or more species of southwestern North America and perhaps also of Central and South America and Africa. The generic limits have been variously interpreted. Watson (1876) considered the differences between

Parkinsonia and *Cercidium* Tulasne (nine taxa currently recognized by Carter; Texas, Sonoran Desert to Peru and Argentina), to be insignificant and merged the two under *Parkinsonia*. Sargent reestablished *Cercidium* and recognized two American species of *Parkinsonia* (*P. aculeata* and *P. microphylla* Torrey) and one species from southwestern Africa (*P. africana* Sonder). The two genera were redefined by Johnston, who considered *Parkinsonia* to include only *P. aculeata* and *P. africana* and *Cercidium* to be composed of nine species (including *C. microphyllum* (Torrey) Rose & Johnston, which was later segregated by Britton & Rose as the monotypic genus *Cercidiopsis*). While reviewing some African members of the Caesalpinioideae, Brenan concluded that *Peltophoropsis scioana* Chiov., of East Africa, along with a new species also from East Africa, and the American species of *Cercidium* (including *Cercidiopsis*) were best included within *Parkinsonia*. Carter (1974a) pointed out that a satisfactory resolution of the generic relationships in this group of plants can only be reached after they have been studied biologically, morphologically, cytologically, and genetically. She added, however, that "*Cercidium* forms a discrete . . . unit confined to the Americas" and that "study of Brenan's comparative chart . . . shows that among the taxa included, *Parkinsonia aculeata* is the most discordant element." Carter suggested, furthermore, that "*Parkinsonia* be considered a monotypic genus comprised of *P. aculeata* Linnaeus" and that "the relationships of the three African species (*P. africana*, *P. anacantha*, and *P. scioana*) be considered further before accepting them as congeneric with *Parkinsonia* and *Cercidium* as proposed by Brenan." Because of the varying concepts of *Parkinsonia*, the description given in the present treatment refers only to *P. aculeata*.

Parkinsonia aculeata, Jerusalem thorn, horsebean, retama, Mexican palo verde, $2n = 14$, is probably indigenous to Texas, New Mexico, Arizona, and Mexico. It is widely cultivated in warm climates throughout the world, particularly in arid regions, and is prone to escape and become naturalized. In our area, it is known at least from Beaufort County, South Carolina, to Key West, Florida, and north and west to southern Georgia and Louisiana.

Putative natural hybrids between *Parkinsonia* and *Cercidium* have been reported by Carter & Rem from Sonora and Guerrero, Mexico (*P. aculeata* × *C. praecox*) and Texas (*P. aculeata* × either *C. texanum* or *C. macrum*).

One of the most striking features of *Parkinsonia aculeata* is the foliage. The leaves are evenly bipinnate, with one to three (rarely to six) pairs of opposite pinnae on a short petiole and rachis. The axes of the pinnae are strongly flattened, narrow, and quite long and drooping, giving the plants a graceful appearance. Numerous, tiny leaflets are borne alternately or oppositely along the edges of the pinnae; these fall during periods of drought, the axes of the pinnae evidently functioning as the principal photosynthetic organ of the plant. The rachises of the pri-

mary leaves (those leaves produced along the current year's growth of a long shoot) are modified into stout, unbranched spines that persist on the branches after the pinnae are shed. On some plants the stipules that subtend primary leaves also are spinescent. Spine-tipped rachises and stipules are not usually found on the secondary leaves (those produced in fascicles on short shoots in the axils of primary leaves), and no other types of spine are found in this species. Carter (1974) pointed out that the primary leaves and spines of *P. aculeata* are different from those of *P. africana* and species of *Cercidium*.

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Tribe CASSIEAE Bronn

6. **Cassia** Linnaeus, Sp. Pl. 1: 376. 1753; Gen. Pl. ed. 5. 176. 1754.

Shrubs, [trees,] or annual or perennial herbs [rarely scrambling or climbing], unarmed [very rarely with prickles or thorns]. Leaves evenly pinnate [rarely absent and the branches then photosynthetic]; petioles with an adaxial groove; leaflets 2 to many, small to large, sometimes sensitive to touch, symmetrical or basally oblique, with a median, eccentric, or marginal midrib [or several parallel veins]; conspicuous sessile or stipitate, variously shaped glands often present on petiole and/or rachis; stipules bristlelike, subulate, linear, falcate, or leafy, persistent or caducous. Inflorescences axillary or terminal, few- to many-flowered, lax or condensed racemes or terminal panicles or the flowers solitary; bracts various, usually of 2 sets, one at base of floral axis, another subopposite pair below each flower. Flowers perfect, rarely imperfect and the plants then polygamous, sometimes enantiostylous, small to large and showy, usually only slightly bilaterally symmetrical (except for the androecium). Calyx lobes 5, ± equal [to strongly unequal], imbricate in aestivation; calyx cup short to nearly absent. Petals 5 [rarely 1 or 2], nearly rotate, ± equal or some smaller, scarcely clawed, yellow (sometimes drying white or pinkish) or less commonly pink, red, or white, sometimes with basal nectar guides, conspicuously veined or not, imbricate. Stamens 10 [rarely reduced to 4 or 5], all fertile or some reduced to staminodes, the fertile ones ± equal or strongly unequal; filaments long to short or nearly absent, ± equal or strongly unequal, glabrous, free, terete [or with swollen areas]; anthers basifixed or infrequently dorsifixed, dehiscing by terminal pores or slits, rarely by basal pores or longitudinal slits, uniform or the abaxial [or adaxial] ones larger, sometimes curved, often constricted above with variously shaped apices. Ovary sessile or stipitate, elongate, often curved, free of the calyx cup, with several to many ovules; style short or elongate, usually curved; stigma terminal, small or rarely ciliate or swollen. Fruits very variable, cylindrical to flat, [rarely winged], indehiscent or dehiscent (sometimes elastically so) and opening along one or both sutures or irregularly dehiscent, woody to coriaceous or membranaceous, with or without septae, sometimes containing pulp. Seeds mostly transverse, sometimes oblique or longitudinal, large to small, flattened or not, ovoid to elongate, rhomboid, rectangular, or trapezoidal; seed coat occasionally smooth, otherwise with fine lines, longitudinally arranged or scattered pits, or closed pleurograms; funiculus long or short. Endosperm present. Embryo spathulate, with flattened or irregularly folded cotyledons. Base chromosome numbers 7 and 8. (Including *Adipera* Raf., *Chamaecrista* Moench, *Chamaesenna* Raf., *Ditremexa* Raf., *Emelista* Raf., *Peiranisia* Raf., and *Psilorhegma* Britton & Rose.) LECTOTYPE SPECIES: *C. fistula* L.[7]; see N. L. Britton & A. Brown, Illus. Fl.

[7] This species has been removed to the segregate genera *Cathartocarpus* Persoon and *Bactyrilobium* Willd. but is accepted generally as the lectotypic species of *Cassia*

No. U. S. Canada ed. 2. 2: 335. 1913; see also A. S. Hitchcock & M. L. Greene, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 152. 1929. (The Greek name of some (lauraceous?) aromatic plant; Theophrastus applied this name to the plant now known as *C. acutifolia* L.)

One of the largest genera of Leguminosae. Bentham (1871) recognized 338 species in his study, the latest worldwide revision, and Irwin (1964) estimated that there have been about 350 species described since that time. The genus is most diverse in the tropics and subtropics, particularly in the Americas. Some species of sections ONCOLOBIUM, PROSOSPERMA, and CHAMAECRISTA extend into the temperate regions of South and/or North America. *Cassia* is very diverse morphologically, and Britton & Rose, following the precedent of Rafinesque, recognized 28 segregate genera as native or introduced to North America. Such fragmentation has not been accepted generally. The subgeneric classification scheme outlined by Bentham, which has been shown to be a quite natural arrangement and is still widely followed, is used here. Bentham's often quoted statement about *Cassia* is worth repeating: "To botanists it presents an excellent instance of a large, widely distributed, much varied, but well-defined group. So natural, indeed, is the genus that, notwithstanding the great contrast in habit between the splendid arborescent Fistulas and some of the weedy herbaceous Prosospermas, or Chamaecristas, and although its principal characters are derived from the pod and the anthers, which both present more diversity than in any other Leguminous genus, yet there is hardly a species which has ever, by any tolerably fair botanist, been falsely or carelessly included or rejected from the genus, except perhaps in the case of a few garden seedlings which had not yet flowered."

Bentham subdivided *Cassia* into three subgenera, eight sections, two subsections, and 30 series. In the southeastern United States, species representing two subgenera and four sections occur indigenously, and another two sections are represented by naturalized species. In addition, a number of exotic species are cultivated in southern Florida; some of these persist from cultivation and may eventually become naturalized.

Subgenus SENNA Bentham (shrubs, trees, or herbs; foliar glands present or absent; leaflets usually rather large; sepals obtuse; androecium variable but usually with one abaxial and three adaxial staminodes, four short fertile adaxial stamens, and two elongate fertile abaxial stamens; anthers basifixed, the tips often constricted and elaborate, dehiscing by apical pores or chinks; fruits variable, dehiscent or not, often with a longitudinal septum, rarely with pulp; seeds usually with a distinct pleurogram on each face, rarely smooth) is represented in our area by nine species in five sections.

Four of these species belong to sect. ONCOLOBIUM Vogel ex Bentham (leaflets several to numerous; glands one per leaf, inserted toward base

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L. Incidentally, *C. fistula* is the twelfth species of *Cassia* enumerated by Linnaeus in the *Species Plantarum*.

of petiole; fruits subcylindric to compressed; seeds transverse or oblique). The closely related *Cassia marilandica* L. (*C. Medsgeri* Shafer) and *C. hebecarpa* Fernald (*Ditremexa marilandica* sensu Britton & Rose; *C. marilandica* of authors, not L.), both commonly known as wild senna, are perennial herbs with 10–20 elliptical to slightly ovate, apically mucronate leaflets per leaf and blackish, elongate, strongly flattened fruits. *Cassia marilandica* can be distinguished from *C. hebecarpa* by the short-appressed, rather than densely long-villous, indument of the ovaries; by the glabrate or short-hirtellous fruits with segments much shorter than broad, rather than loosely villous fruits with segments as long as broad; and by the plump, obovoid, rather than flattened, quadrate seeds. *Cassia marilandica* is widespread in our area, occurring from Pennsylvania to Iowa, south to Florida and Texas. *Cassia hebecarpa* is more northeastern in its distribution, ranging from New England to Wisconsin, southward to North Carolina, eastern Tennessee, northern Georgia, and Alabama.

Cassia occidentalis L. (*Ditremexa occidentalis* (L.) Britton & Rose), coffee senna , $2n = 28$, a tall annual herb with 6–12 tapering-ovate leaflets per leaf, globose petiolar glands, and elongated, compressed fruits with thickened sutures, is a native of tropical Central and South America that has become naturalized from Florida to Texas, north to Virginia, Indiana, Illinois, Iowa, and Kansas; it is also introduced in the tropics of the Old World. *Cassia ligustrina* L. (*Ditremexa ligustrina* (L.) Britton & Rose), a small shrub with 12–16 narrowly ovate or lanceolate, basally oblique leaflets per leaf and conic-cylindrical petiolar glands, occurs mostly in hammocks in central and southern Florida and also on the Greater Antilles, Bermuda, and Grand Cayman Island.

Cassia obtusifolia L. (*C. Tora* of authors, not L.; *Emelista Tora* sensu Britton & Rose), sickle-pod or coffee-weed, of sect. PROSOSPERMA Bentham (leaflets 2 to numerous, rather large; petiolar gland(s) situated between the lowest pairs of leaves; fruits subterete, 4-angled, or compressed-lomentaceous; seeds longitudinal) is a pantropical weed that extends northward in eastern North America from Florida and Texas to Pennsylvania, Indiana, Michigan, Illinois, Missouri, and Kansas. According to Brenan (subfamily references), this species has generally been confused with *C. Tora* L., a species confined to Asia. *Cassia obtusifolia* can be separated from the other species of *Cassia* in our area by its annual duration; broad, obovate leaflets with a cylindrical gland situated between the lowest pair; few-flowered, seemingly axillary inflorescences; linear, curved fruits; and rhomboid seeds. The embryo of *C. obtusifolia*, unlike that of most other species of the genus, has folded cotyledons.

Section CHAMAESENNA DC. (leaf glands situated between the lower pair or pairs of leaflets or absent; leaflets moderate-sized to large; fruits usually compressed or flattened; seeds flattened) is represented in our area by *Cassia bahamensis* Miller (*Peiranisia bahamensis* (Miller) Britton & Rose). This species is a shrub with basally oblique, ovate, elliptic, or obovate, mostly mucronate leaflets that have small glands scattered on the lower surfaces and along the midrib on the upper surfaces and with large,

globose glands on the leaf rachises between the lower pairs of leaflets. It occurs mostly in pinelands in southernmost Florida in the vicinity of Miami, the Everglades, and on some of the southwestern Florida Keys (No Name Key, Big Pine Key, Key West); it also occurs on Cuba and some of the Bahama Islands. Several species of sect. CHAMAESENNA are commonly cultivated in southern Florida, including *C. alata* L. (*Herpetica alata* (L.) Raf.), a native of tropical America, and *C. didymobotrya*

FIGURE 5. **Cassia.** a–j, *C. bahamensis*: a, flowering branch with immature fruits, × ½; b, front view of opening flower bud to show sepals and aestivation of petals, × 2; c, flower, × 2; d, upper staminode (1 of 3), × 4; e, functional lateral stamens (2 of 4) opening by terminal pores, × 4; f, functional lower stamen (1 of 2), × 4; g, lower staminode, × 4; h, gynoecium, × 4; i, portion of immature fruit opened to show developing seeds with threadlike funiculi, × 3; j, oblique view of seed — note lateral, closed pleurogram, × 4. k, l, *C. obtusifolia*: k, fruit, × ½; l, seed — note narrow, closed pleurogram, × 4. m–o, *C. fasciculata* var. *fasciculata*: m, pinnately compound leaf with persistent stipules, × ½; n, bud to show tapering-acute sepals, × 2; o, seed marked with numerous small pits arranged in rows, × 4.

Fresenius (*Chamaesenna didymobotrya* Small), of tropical Africa; Small noted the occurrence of the latter species in vacant lots in Miami, Florida.

Cassia surattensis Burman f. (*C. glauca* Lam., *C. suffruticosa* König, *Psilorhegma suffruticosa* (König) Britton), of sect. PSILORHEGMA Bentham (stamens 10, all fertile; filaments short; fruits flattened), is a native of tropical Asia widely cultivated in tropical regions and occasionally naturalized in hammocks in southern Florida.

Cassia bicapsularis L. (*Adipera bicapsularis* (L.) Britton & Rose) of sect. CHAMAEFISTULA DC. (mostly shrubs; foliar glands situated between the lower pairs of leaflets or absent; fruits terete, turgid, dehiscent along the adaxial suture or not; seeds transverse, separated by transverse septae) occurs along canal and road banks and in marshes in southern Florida, as well as in the West Indies, Mexico, and Central and South America. This species is distinctive in its relatively large, obovate leaflets, globose foliar glands, large yellow flowers, two abaxial stamens with greatly elongated filaments, and mostly straight, cylindrical fruits with ovoid, slightly flattened, smooth or faintly pitted seeds. *Cassia corymbosa* Lam. (*Adipera corymbosa* (Lam.) Small) a native of Argentina and Uruguay, has fruits and seeds similar to those of the preceding species, but it has slightly smaller flowers, narrowly ovate leaflets, and cylindrical foliar glands. According to Small, this species is occasionally adventive along the Coastal Plain from Georgia to Louisiana and Tennessee.

The largest number of species of *Cassia* in the southeastern United States belong to sect. CHAMAECRISTA DC. of subg. LASIORHEGMA Bentham (fruits elastically dehiscent; funiculus short; seeds with numerous pits usually arranged in rows). Bentham divided sect. CHAMAECRISTA into two subsections, subsect. XEROCALYX, which Irwin has elevated to the rank of section, and subsect. LEIOCALYX; all of the southeastern species belong to the latter and are annual or perennial, sometimes suffrutescent herbs with small, mostly numerous leaflets, persistent stipules, several-flowered axillary racemes, membranaceous, pointed calyx lobes, and an androecium of unequal stamens with polliniferous anthers. In their treatment of the Caesalpinioid legumes for the *North American Flora*, Britton & Rose (following Greene) recognized the genus *Chamaecrista* Moench with 111 species, subdividing them into 17 groups of undesignated rank. Five of their groups occur in our area. *Cassia rotundifolia* Persoon (*Chamaecrista rotundifolia* (Persoon) Greene), the only species of group Rotundifoliae, is a prostrate perennial with leaves having only two leaflets and lacking petiolar glands. It has been reported from near Orlando, Florida, as well as from Mexico, Central and South America, the West Indies, and western Africa. *Cassia serpens* L. (*Chamaecrista serpens* (L.) Greene), of group Pilosae, has been reported from Florida by Ward. This species is a tap-rooted, woody-based herb with cylindrical petiolar glands and strongly unequal petals; it occurs primarily in the West Indies and Central and South America. *Cassia keyensis* (Pennell) MacBride (*Chamaecrista keyensis* Pennell), of group Lineatae, is a soft-hirsute, suffrutescent perennial with many branches from a contorted rootstock and large yellow flowers. It

has been considered endemic to Big Pine Key, No Name Key, and Key West, Florida, but Ward has recently included it within *C. grammica* Sprengel, a West Indian species.

The remaining species of sect. CHAMAECRISTA in the southeastern United States belong to group Fasciculatae, which has been treated quite variously in floras (cf. Small, Britton & Rose, Fernald, Gleason, Radford *et al.*, and Long & Lakela) and in recent reviews and lists (Turner, Pullen, Ward). Two species complexes can be recognized. The first, with very short pedicels, stalked petiolar glands, and small flowers with five stamens and short anthers, includes *Cassia aspera* Muhl. ex Ell. (petiolar gland cylindrical, "odd petal" only slightly longer than the others), which occurs in pinelands and sandy areas from southeastern South Carolina along the coast of Georgia to the Florida Keys, and *C. nictitans* L. (*Chamaecrista multipinnata* Pollard, *Ch. procumbens* (L.) Greene), wild sensitive plant (head of petiolar gland globose, "odd petal" nearly twice as long as the others), which is found in acid, sandy or rocky soils of open woods, upland slopes, ridges, bluffs, prairies, fallow fields, and open thickets from Florida to Texas, north to Massachusetts, Vermont, New York, Ohio, Indiana, Illinois, Missouri, Kansas, and Oklahoma. The latter is especially variable in pubescence, and several varieties have been proposed.

The second complex of group Fasciculatae includes species that have longer pedicels, mostly sessile petiolar glands, larger flowers, and ten elongated anthers. Eight species of this complex of "partridge peas" were recognized in North America by Britton & Rose, with six in our area. These are *Chamaecrista brachiata* Pollard, *Ch. fasciculata* (Michx.) Greene, *Ch. robusta* Pollard, *Ch. depressa* (Pollard) Greene, *Ch. mississippiensis* Pollard, and *Ch. littoralis* Pollard. *Chamaecrista Deeringiana* Small & Pennell was included by Britton & Rose with some perennial species of southwestern North America in their group Deeringianae, but this species is now considered to be a member of the *Cassia fasciculata* complex. Recent authors have interpreted this complex as a single polymorphic species, and they have either considered it meaningless to attempt to account in a taxonomic system for the variation that occurs in this group, or they have recognized a number of varieties that admittedly intergrade with one another. This complex as it occurs in the United States was most recently reviewed by Pullen (unpublished Ph.D. thesis), who considered *C. Deeringiana* (Small & Pennell) MacBride (scattered from central Georgia to southern Florida and southwestern Alabama) to be distinct from *C. fasciculata* Michx., which he subdivided into eight varieties. According to Pullen, five of these varieties occur in our area: *C. fasciculata* var. *fasciculata* (Florida to Texas, north to Massachusetts, New York, Ontario, Ohio, Indiana, Wisconsin, Minnesota, and South Dakota), var. *littoralis* (Pollard) MacBride (North Carolina, Georgia, northern Florida, Alabama, Mississippi, Louisiana, and Texas), var. *robusta* (Pollard) MacBride (mostly sympatric with var. *fasciculata*, but not extending into peninsular Florida), and var. *Tracyi* (Pollard) MacBride (Georgia, northwestern Florida, Alabama, Mississippi, Arkansas, Louisiana, and Texas; apparently disjunct

in Illinois). The name of the fifth variety (ranging from Delaware to southern Florida) is based on *Cassia brachiata* Pollard, but Pullen's combination is still unpublished.

Several species of subg. CASSIA (subg. FISTULA Bentham), including *Cassia fistula* L., golden shower, *C. grandis* L. f., pink shower, *C. nodosa* Hamilt., *C. javanica* L., and *C. renigera* Wall. ex Bentham, are cultivated in southern Florida. Members of this subgenus are trees with leaves lacking foliar glands; the sepals are obtuse; the ten stamens are all fertile, but the three abaxial ones are at least twice as long as the seven adaxial ones; the anthers are not basifixed, and they open (within the same flower) by incomplete longitudinal slits and by basal pores; the fruits are indehiscent and often contain pulp; and the seeds are smooth, transversely arranged in the fruits, and separated by complete septae.

The flowers of many species of *Cassia* show enantiostyly (the occurrence of left- and right-handed flowers), with the flowers differing in the direction in which the style is bent and in the relative position of the different calyx lobes and petals. This phenomenon is particularly evident in the *Cassia fasciculata* complex, where the larger "odd" petal (which is not the banner petal) occurs on the side of the flower that is away from the stem.

The androecium of *Cassia* is remarkably diverse in the fertility, size, shape, mode of dehiscence, and, to a lesser degree, number of stamens. In subg. CASSIA (subg. *Fistula* Bentham) there are ten stamens in two whorls, all with fertile anthers. Stamens of the outer whorl are of two types — the three abaxial ones have very elongate, S-curved, sometimes nodose filaments and large anthers, while the two adaxial ones have short, straight filaments and small anthers. All anthers of the inner whorl dehisce by two incomplete subapical and two incomplete subbasal slits. The five stamens of the inner whorl are of intermediate size and have basally 2-spurred anthers that dehisce by subbasal pores located at the tips of the spurs. The androecium of members of subg. LASIORHEGMA consists of ten, or infrequently five, stamens that are all fertile and alike in form, structure, and dehiscence, although they differ somewhat in size within a flower. The filaments are rather short and the anthers are basifixed, apically bilobed, and dehiscent by apical chinks. The anthers of subg. LASIORHEGMA are unique in that the lateral sutures are prevented from opening by rows of closely coiled and interlocked trichomes. Subgenus SENNA is more variable in androecial structure, and some species may have ten stamens that are all fertile and more or less alike. However, in most species of this subgenus in our area, three adaxial stamens are reduced to small, spathulate staminodes; four lateral stamens are fertile and have filaments and anthers of varying lengths; and three abaxial stamens have greatly elongated, curving filaments and large, polliniferous anthers. In some species the central abaxial stamen is smaller than the others and may lack pollen. The fertile anthers in subg. SENNA dehisce by terminal pores or chinks and are tipped by modified, often elaborate structures that presumably have some function

in pollination. For a detailed review of the androecium of *Cassia*, see the series of papers by Venkatesh.

Little is known about plant-insect relationships involving *Cassia*, but in view of the diversity of the flowers, particularly of the androecium, and the frequent presence of extrafloral nectaries (the foliar glands), it would seem that this is a good area for future investigations. The few reports of pollination indicate that there are several different systems. Stevens reports that in *C. marilandica* bees land on the carpel and three lower stamens and then bite open the four middle anthers, removing the pollen to their pollen baskets. Charles Robertson, however, observed that on this species, and on *C. Chamaecrista*, bees stroke the anthers with their mandibles, thus "milking" the pollen out of the terminal pore. In any case, the two long stamens on either side of the style furnish pollen for pollination. A case of "buzz" pollination is reported by Buchmann in *C. Quiedondilla*. In this case bees land on the flower and curl their bodies tightly over the long pollinating anthers; they then vibrate their indirect flight muscles, causing a small cloud of pollen to come out of the terminal pores.

The seeds of *Cassia* are also of taxonomic value. In subg. CASSIA they are smooth, shiny, and sometimes marked with faint to distinct cracks in the outer seed coat. These cracks may be more or less uniform on the seed or more prominent on the faces. Occasionally, seeds may have a few faint, minute pits, and in some species there is a line running from the hilum across one or both faces to the top of the seed. Apparently the majority of species of subg. SENNA have seeds with a distinct raised or depressed and/or differently colored area called a pleurogram (areole, *lineafisural*, face area) on each side. The shape and size of the pleurogram varies considerably from species to species, but it is always closed and thus differs from the U-shaped pleurograms found in most species of Mimosoideae. The seeds of *C. bicapsularis* and *C. corymbosa*, of subg. SENNA, lack pleurograms and greatly resemble seeds typical of subg. CASSIA; these and related species should be examined more closely. The seeds of plants of subg. LASIORHEGMA seem always to be marked with numerous, usually prominent pits that may be arranged in longitudinal rows or randomly scattered over the surface. For a summary of the internal morphology of seeds of *Cassia*, see Okpon. Polyembryony and facultative apomixis have been observed in several species of the largely Australian sect. PSILORHEGMA of subg. SENNA. Janzen has made a detailed study of the predation of *C. grandis* seeds by bruchid beetle larvae.

Chromosome numbers are known for about 100 species representing all subgenera and sections of *Cassia*. The genus is rather complex cytologically, with several base numbers, polyploidy, and aneuploidy. Within subg. CASSIA, sporophytic numbers of 24 and 28 have been reported. Subgenus SENNA is diverse, with the following sporophytic numbers reported for each section: sect. CHAMAEFISTULA, 24, 26, 28, 52 (with 28 the most frequent count); sect. ONCOLOBIUM, 24, 26, 28, 56 (with 28 again predominant and some of the early counts of 24 and 26 questionable); sect. PROSOSPERMA, 22, 26, 28 (the uniglandular form of *C. obtusi-*

folia of the southeastern United States and the West Indies is $2n = 28$, while the biglandular form of northern South America is $2n = 26$); sect. CHAMAESENNA, 16, 24, 28; and sect. PSILORHEGMA, 14, 28, 42, 56 (see Randell for an analysis of this largely Australian group). Section ABSUS of subg. LASIORHEGMA appears to be uniformly $2n = 28$. The two subsections of sect. CHAMAECRISTA consistently differ in base chromosome number, with $x = 7$ and $2n = 14$ in subsect. XEROCALYX and $x = 8$ and $2n = 16$ or rarely 32 or 48 in subsect. LEIOCALYX. Irwin & Turner suggest that the base chromosome number in *Cassia* is 7, with the derived numbers 13, 12, and 11 arising by aneuploid loss from various euploid levels. The base number of 8 in subsect. LEIOCALYX presumably would have arisen by the aneuploid gain of one chromosome.

The drug senna, used as a cathartic, comes from the dried leaves of *Cassia Senna* L., Alexandrian senna, and *C. angustifolia* Vahl, Tinnevelly senna (nomenclature that of Fairbairn & Shrestha). The leaves or fruits of a number of other species, including *C. fistula*, *C. grandis* L. f., *C. javanica* L., *C. marilandica*, *C. moschata* H.B.K., and *C. Sophera* L., are used locally for the same purpose. Infusions of the leaves of *C. alata*, *C. absus* L., *C. sericea* Sw., *C. Sophera*, *C. obtusifolia*, and *C. Tora* L. are used in treating skin diseases, particularly ringworm. *Cassia laevigata* Willd., *C. obtusifolia*, *C. occidentalis*, and *C. sericea* have been used locally as coffee substitutes. A mordant used in combination with blue dyes is obtained from the seeds of *C. Tora*. The roots of *C. nodosa* Lam. are used locally as a soap substitute. The wood of several species, including *C. javanica*, *C. nodosa*, *C. siamea* Lam., *C. Sieberiana* DC., and *C. timoriensis* DC., is hard, heavy, and often beautifully grained and is used locally. The pods of *C. grandis* are high in pectin, and a gum similar to guar (obtained from *Cyamopsis tetragonoloba*) can be obtained from the seeds of *C. occidentalis*; both of these species have been suggested as potential commercial crops. A number of species, including *C. alata*, candelabra bush, *C. bicapsularis*, Christmas bush, *C. fistula*, golden shower, *C. grandis*, pinkshower cassia, *C. javanica* (including *C. nodosa* Roxb.), pink cassia, *C. siamea*, *C. spectabilis* DC., yellow shower, and *C. suratten-sis*, are commonly cultivated in tropical and subtropical regions, including southern Florida. The rainbow shower tree, commonly seen in Honolulu, is a hybrid between *C. fistula* and *C. javanica*.

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Tribe AMHERSTIEAE Bentham emend. J. Léonard

7. **Tamarindus** Linnaeus, Sp. Pl. 1: 34. 1753; Gen. Pl. ed. 5. 20. 1754.

Medium to large, unarmed, evergreen trees with short, thick trunks, rounded crowns, and widely spreading branches; twigs zigzagged, pubescent when young; bark rough, fissured; buds solitary, sessile, the terminal one absent. Leaves alternate, evenly once pinnate, shortly petiolate, the petiole with a basal pulvinus; leaflets opposite, small, numerous, the apices rounded and shortly mucronate, folding against the rachis at night, translucent dots absent, the margins ± parallel, the bases asymmetrically rounded, nearly sessile, with a wrinkled basal pulvinus; stipules free, asymmetrical, caducous. Inflorescences terminal or axillary, pendulous, several-flowered, rather lax racemes shorter than the leaves; bracteoles *2*, well developed, bright pink, inclosing young flower buds, valvate, caducous. Flowers perfect, moderate-sized; buds red. Calyx lobes 4, equal, reflexed at anthesis, white to pale yellow on adaxial surface, reddish on abaxial surface, more than twice as long as the turbinate floral tube, imbricate in aestivation. Petals unequal, the upper 3 elliptic to obovate, yellow-gold with red veins, recurving widely, slightly exceeding the calyx lobes, the lower *2* minute, scalelike. Fertile stamens 3, exserted above the petals, their filaments curving adaxially, monadelphous for half their

length into a sheath open on the adaxial side, with teeth representing staminodia alternating with free portions of filaments; anthers dorsifixed, versatile, opening by longitudinal slits. Carpel long-stipitate, the gynophore adnate to the floral tube; style elongate, stout, curving adaxially, swollen apically, and topped by a tuft of stigmatic papillae. Fruit pendent, indehiscent, sausage-shaped with irregular constrictions, somewhat compressed laterally, reticulate, brown at maturity, with a dry, thin outer layer, a pulpy middle layer including several fibrous strands, and a coriaceous inner layer forming septae between the seeds, the outer layer cracking into irregular plates as the fruits dry. Seeds 1–10 per fruit, rhomboid, laterally compressed, shiny chestnut brown, with a continuously margined pleurogram on each face; seed coat hard, the outer layer becoming mucilaginous when wet; embryo large; endosperm absent. Base chromosome number 12. TYPE SPECIES: *T. indica* L. (Name from Arabic *tamr*, date, and Latin *indus*, Indian.) — TAMARIND.

A single species, *Tamarindus indica*, tamarind, widely cultivated in tropical areas. Its native range is impossible to determine at present, but it is indigenous to the savannas of Africa and was probably introduced into India at an early date. Additional species described from northeastern tropical Africa are best included with *T. indica*, according to Brenan. The tamarind is cultivated in southern Florida as a shade tree and for its fruits. It has evidently become naturalized in Lee County and on some of the Florida Keys.

The inflorescences of *Tamarindus indica* are pendulous, but the flowers are not resupinate. Consequently, the flowers are in a morphologically upside-down position. At anthesis the floral tube bends abaxially (i.e., upward, in relation to the ground), so that the axis of the flower is more or less perpendicular to the ground. In this position the androecial sheath and the carpel arch obliquely upward over the three large petals, the inner surfaces of which form a horizontal landing place for pollinators. As an insect lands on the petals and crawls toward the opening of the nectariferous floral tube, any pollen on the insect's back is transferred to the stigma and a new load is acquired from the three fertile anthers.

The tamarind is a most useful plant. The trees are evergreen and very ornamental; large specimens are resistant to strong winds and light frost. The wood, hard, heavy, and fine-grained, is used locally for tools and cabinet work and makes an excellent charcoal (formerly used in gunpowder). However, *Tamarindus* is usually grown as a fruit tree. The pulp of the ripe fruits has high concentrations of both sugar and tartaric acid; it is eaten fresh or extracted and used in making fruit drinks, curries, chutneys, candy, ice cream, sauces, sweetmeats, preserves, jellies, medicinal preparations, and brines for pickling fish. The pulp is one of the major ingredients in Worcestershire sauce. Overripe fruits may be used to remove tarnish from copper and brass. The seeds are edible and can be made into flour. Sizing for cloth, paper, and jute products is made from the seeds, as well as vegetable gum and oil. The leaves and

green twigs are used as flavoring agents, and the leaves and flowers are eaten in salads. The leaves yield a yellow dye.

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Tribe CERCIDEAE Bronn, "Cerceae"

8. **Cercis** Linnaeus, Sp. Pl. 1: 374. 1753; Gen. Pl. ed. 5. 176. 1754.

Deciduous, rather flat-topped, unarmed, small to medium-sized trees or shrubs with zigzagged branches; bark with small, loose scales; axillary buds paired, superposed, the upper ones shortly stalked, the lower ones sessile and covered by top of leaf scar, the bud scales shortly fringed; vegetative buds 2-scaled, at nodes toward tip of growth of previous season, flowering buds several-scaled, at nodes toward base of growth of previous season and on older growth; terminal bud lacking, the growth consequently sympodial; leaf scars raised, decurrently ridged from the nodes, round-triangular, fringed at the top, with 3 bundle traces. Leaves appearing simple (evidently derived from fusion of 2 leaflets), alternate, 2-ranked, long-petiolate, the largest at tips of branches; blades with cordate bases, entire margins, and tapering-acute [obtuse or emarginate] apices, with 5, 7, or 9 prominent palmately arranged veins; petioles swollen at each end; stipules small, scalelike, caducous, leaving no scar. Inflorescences sessile umbel-like clusters [or elongate racemes] along growth

of the previous and earlier years and on the trunk, flowering before and as the leaves expand; pedicels jointed, colored like the calyx; bracts small, scalelike, often imbricate at base of inflorescences. Flowers perfect, 5-merous, papilionaceous in appearance. Sepals connate into a bilaterally symmetrical, basally enlarged, magenta, persistent floral cup; calyx lobes 5, short, triangular. Petals 5, free, clawed, purplish pink or rarely white, inserted on the floral cup, the upper, adaxial, banner petal smallest and inclosed in bud by the 2 lateral wing petals and 2 keel petals. Androecium of 10 free stamens, inclosed by the keel petals; filaments thickened, pubescent below, persistent, inserted on the floral cup, the alternate ones shorter; anthers versatile, all fertile, 2-locular at maturity, opening by longitudinal slits. Ovary shortly stalked, inserted obliquely at base of floral cup; style tapering, curved upward; stigma terminal, knoblike; ovules numerous. Fruit stalked, laterally flattened, tapering at each end, narrowly winged on the adaxial side, prominently veined, reddish, shiny, often tardily dehiscent along both sutures, the margins parallel or the abaxial one curved inward at each end. Seeds usually 3–6 on slender funicles, orbicular to oblong, compressed; seed coat crustaceous, bright red-brown; embryo surrounded by a thin layer of endosperm; cotyledons flattened, orbicular to oblong; radicle superior. Base chromosome number 14. TYPE SPECIES: *C. Siliquastrum* L.; see C. S. Sargent, Silva N. Am. 3: 93. 1892. (Name from Greek *kerkis*, weaver's shuttle, perhaps alluding to the shape of the fruit; Theophrastus used this name for a leguminous plant, evidently *C. Siliquastrum*.) — REDBUD, JUDAS TREE.

About eight species in four widely separated areas: *Cercis canadensis* L. in eastern North America southward to northeastern Mexico; *C. occidentalis* Torrey ex Gray in western North America; *C. Siliquastrum* in southern and eastern Europe (probably indigenous only from Turkey eastward to Afghanistan); and five species described from China. The Chinese species are *C. chinensis* Bunge (widely distributed in temperate China, most abundant in western Hupeh and eastern Szechwan), *C. racemosa* Oliver (eastern Szechwan and adjacent Hupeh), *C. Chuniana* Metcalf (Kwangsi), *C. Chingii* Chun (Anhwei and northern Kwangtung), and *C. pauciflora* Li (Szechwan). The taxa of eastern North America and eastern Asia are morphologically similar to one another, as are those of western North America and Europe.

Cercis canadensis, redbud or (in parts of our area) Judas tree, ranges from southern Connecticut and New York south to central Florida and west to Michigan, southern Wisconsin, Iowa, eastern Nebraska and Kansas, much of Oklahoma and Texas (except for the panhandles), and northeastern Mexico (Tamaulipas, Coahuila, Nuevo León, San Luis Potosí, Hidalgo). The only report of the species outside of cultivation in Canada is that of a tree that formerly grew on Pelee Island in Lake Erie, Essex County, Ontario. Throughout most of the range of the species, the mature leaves are thin, dull green on both surfaces (young leaves are

glossy and reddish) and have tapering-acute apices; these plants, var. *canadensis*, occur from the northern and eastern limits of the species southwestward to eastern Texas (see Turner and Correll & Johnston, Man. Vasc. Pl. Texas). The young leaves are usually pubescent below, with some trichomes remaining on the mature leaves. Individuals with glabrous leaves are f. *glabrifolia* Fernald. Southwestward from the Arbuckle Mountains of Oklahoma, some or all populations have leaves that are rather coriaceous, rich deep green, shiny, distinctly glaucous above, and with rounded, obtuse, or emarginate apices. Plants of this kind with glabrous petioles and young branchlets are var. *texensis* (Watson) Rose (Edwards Plateau and north-central Texas to the Arbuckle Mountains of Oklahoma) and those with densely woolly-tomentose petioles and branchlets, var. *mexicana* (Rose) Hopkins (Crockett and Val Verde counties, Texas, to the Trans-Pecos and northeastern Mexico) (cf. Turner). The species is particularly variable in the Arbuckle Mountains and north-central Texas. Edgar Anderson thought this variability to be

FIGURE 6. **Cercis.** a–j, *C. canadensis* var. *canadensis*: a, leaf — note pulvinus at apex of petiole, × ½; b, flower, upper banner petal is innermost, × 3; c, flower in partial section, petals removed, 6 stamens shown — note gynophore of gynoecium adnate to floral cup, × 4; d, wing petal, × 3; e, keel petal, × 3; f, banner petal, × 3; g, branch with fruits after fall of leaves, × ¼; h, fruit, × ½; i, seed, × 4; j, embryo from soaked seed, × 3.

the result of introgression between the typical variety and varieties of the Southwest.

Cercis canadensis var. *canadensis* is most often seen as a small tree, but mature specimens can be moderate-sized trees with broad, rather flat-topped crowns, and the largest recorded plants are more than 16 m. tall, with a crown spread of 13 m. and a trunk diameter at breast height of 0.8 m. (For a photograph of a large specimen, see Plummer & Lindsey.) Redbud is one of the earliest woody plants to flower, and it is in spring, when the plants are in full bloom, that the abundance of this species in much of the eastern United States is apparent. The flowers are papilionaceous in appearance (but the banner petal is innermost). They are borne in sessile umbel-like clusters along the naked growth of the previous year and on older branches and are pollinated mostly by various long- and short-tongued bees. Older trees are especially cauliflorous, and large areas of the trunk can be covered by inflorescences. Flowering begins before the leaves expand, and the flowering period seems longer than it really is, since the magenta floral tubes are conspicuous for some time before the lavender-pink petals open. Varietas *canadensis* has a rather wide tolerance of environmental conditions, although it prefers strong sunlight and soils that have good drainage and are derived from limestone or sandstone. In the northern and eastern part of its range, it is found in open woodlands, borders of woods, thickets, limestone glades and openings, and along rocky streams and bluffs. Toward the south and west, it occurs in rich woods, ravines, bottomlands, and rich soil along streams. Varietas *canadensis* and var. *texensis* are evidently ecologically separated in the region where their distributions overlap, with the former occurring on sandy soils and the latter on calcareous soils.

Eastern redbud and flowering dogwood, *Cornus florida*, have similar geographical distributions and often occur together (perhaps even in some localities in Mexico). Although redbud is usually nearly past flowering when the dogwood begins to bloom, in exceptional years both are simultaneously in full flower, producing a spectacular show of spring color. In some localities redbud flowers at about the same time as some of the shadbushes (*Amelanchier*) and wild plums (species of *Prunus* sect. Prunocerasus).

The fruits of *Cercis canadensis* are strongly flattened and persist on the plants until after the leaves have fallen. They are evidently dispersed by wind blowing them off the branches at various intervals during the fall and winter. Late in the season, while the fruits are still on the plants or after they have fallen, the sutures open on some of the fruits, releasing the seeds; in the case of those fruits that do not open, seed release is effected by the decay of the fruit wall.

Cercis canadensis var. *canadensis* is commonly cultivated in temperate regions and is hardy considerably north of its natural range. White-flowered plants, f. *alba* Rehder, are becoming common in cultivation, and plants with rather unsightly double flowers, f. *plena* Sudworth ex Schneider, are also known. Several cultivars, with the flowers a paler color than

usual, have been named. The eastern redbud does not grow very well in England and southern Europe, where the true Judas tree, *C. Siliquastrum*, is commonly cultivated and extensively naturalized. It is said that the Judas tree, both in cultivation and in the wild, produces a show of spring flowering as spectacular as that of our eastern redbud; this species does not do well in our climate and is rarely cultivated here. *Cercis occidentalis* and *C. canadensis* vars. *texensis* and *mexicana* are seldom cultivated outside the areas in which they occur naturally. The Chinese redbud, *C. chinensis*, is occasionally cultivated in eastern North America and is hardy at least as far north as Boston. Ernest Wilson considered *C. racemosa* to be one of the very best and most beautiful of the flowering trees introduced by him into cultivation, but it is rarely grown in North America and is not hardy northward. Bean says that there are a few living plants in England. (The other Chinese species are evidently not in cultivation in North America.)

Cercis is a very distinctive genus within the Caesalpinioideae. Because of the "simple" leaves that are actually derived from the fusion of two leaflets (see Fries), the gamosepalous calyx with valvate calyx lobes, the ten free stamens, and the dorsifixed anthers that open by longitudinal slits, *Cercis* is grouped with *Bauhinia* L. sensu lato in tribe Cercideae. Several species of *Bauhinia* are commonly cultivated in southern Florida, but none are known to escape.

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STYRACACEAE HARDY IN TEMPERATE NORTH AMERICA [1]

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STYRACACEAE Dumortier, Anal. Fam. 28, 29. 1829, "Styracineae," nom. cons.

(STYRAX FAMILY)

Evergreen or deciduous trees or shrubs, usually with stellate (or lepidote) pubescence. Leaves simple, alternate, exstipulate, with entire, serrate, dentate, or occasionally lobulate margins, the venation pinnate. Flowers perfect, actinomorphic; inflorescences often reduced, the flowers usually arranged in simple or sometimes branched, terminal and/or axillary racemes, corymbs, or panicles, occasionally solitary or in few-flowered fascicles. Calyx often articulated at the base, synsepalous, tubular, subentire or 4- or 5-toothed or -lobed; calyx tube entirely free to completely adnate to the ovary. Corolla sympetalous, 4- or 5-lobed (rarely more), often united into a tube only at the base; insertion of the corolla hypogynous (ovary superior) to epigynous (ovary inferior), the lobes valvate or imbricate in bud. Stamens usually twice the number of the corolla lobes, sometimes more, epipetalous, inserted in 1 whorl on the base of the corolla (or rarely at the base of the ovary), the filaments usually connate into a tube below, free above; anthers 4-locular. Gynoecium syncarpous,

[1] This treatment of the Styracaceae is the second contribution in a series of treatments of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum of Harvard University and the purpose of which is to provide a modern, accurate account of the woody plants encountered in cultivation in the cooler temperate regions of North America. It is hoped that these treatments will eventually form the basis of a new manual of cultivated woody plants. The first paper in this series was published in the Journal of the Arnold Arboretum **56**: 1–19. 1975. Reference should be made to the introductory paragraphs of that paper for matters concerning area covered, taxa included, and the general philosophy of these treatments.

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Special thanks and gratitude are also extended to an anonymous donor, whose generous gift for this project has made and continues to make this work possible. In addition, our deepest thanks are extended to the Director and trustees of the Stanley Smith Horticultural Trust for a grant that has made possible the preparation of illustrations to accompany these treatments. S. A. S.

the ovary superior and completely free to inferior and completely adnate to the calyx tube, 3–5-locular, often 1-locular above, each locule with 1 to many ovules on axile placentae; style 1, slender, terminated by a usually 3–5-lobed stigma. Fruits dry, often woody, indehiscent or dehiscent; seeds 1 to many, the usually straight embryo with broad cotyledons embedded in fleshy endosperm. TYPE GENUS: *Styrax* L.

Thirteen genera and about 150 species distributed primarily in eastern Asia to western Malesia, tropical South America, and North America, primarily in the southeastern United States. One species (*Styrax officinale* L.) occurs in the Mediterranean region, while about three additional species are native to Africa.

The genus *Sinojackia* H. H. Hu, included by Rehder (1942) in his *Manual*, has been excluded from the present treatment, since evidence of its hardiness and cultivation in our area has not been located. Apparently, only *S. rehderiana* Hu is grown in North America at the present time; we have records of its inclusion in the collections of the Strybing Arboretum in San Francisco.

Closely related to *Rehderodendron* and *Pterostyrax*, *Sinojackia* is distinguished from both of these genera by its flowers on slender pedicels in 3–5-flowered racemes terminating leafy, lateral branches, by its stamens with the connectives produced beyond the anthers, and by its ovoid, woody, unribbed fruits, 1.5–2.5 cm. long.

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KEY TO THE GENERA OF STYRACACEAE IN CULTIVATION

1. Ovary ± inferior, adnate to the calyx tube; insertion of the corolla epigynous; fruits sometimes surmounted by the persistent calyx lobes; pedicels articulated at the base of the calyces. ..... 2.

2. Pith chambered; flowers solitary, in few-flowered fascicles, or rarely in irregular racemes above leaf scars on second-year branchlets; corolla with 4 or rarely 5 lobes; fruits conspicuously 2- or 4-winged. . . . . 1. *Halesia*.

2. Pith continuous; flowers in racemose or paniculate inflorescences above leaf scars on second-year branchlets or in paniculate or corymbiform inflorescences terminating short, lateral branchlets from second-year wood; corolla with 5 lobes; fruits obscurely ribbed, 5-winged, or large, woody, and variously ribbed, or smooth. . . . . 3.

3. Stamens subequal; flowers several to numerous, in paniculate or corymbiform inflorescences terminating short, lateral branchlets; fruits small, 8–17 mm. long, obscurely ribbed or 5-winged. . . . . 2. *Pterostyrax*.

3. Stamens of 2 unequal lengths; flowers few, in racemose or paniculate inflorescences above leaf scars; fruits large, (4–)6–8.5 cm. long, smooth or variously ribbed, not winged. . . . . 3. *Rehderodendron*.

1. Ovary ± superior, usually adnate basally to the calyx tube, rarely entirely free; insertion of the corolla hypogynous to perigynous; fruits subtended by the persistent calyces; pedicels not articulated at the base of the calyces. . . . . 4. *Styrax*.

1. **Halesia** Ellis ex Linnaeus, Syst. Nat. ed. 10. 2: 1044, 1369. 1759, nom. cons.[2]

Deciduous trees or shrubs, the branchlets with chambered pith; winter buds ellipsoidal to ovoid, pubescent; bark brownish, gray, or blackish, becoming deeply cleft on older trees. Leaves petiolate, the blades chartaceous, ovate-oblong, elliptic, or obovate, with acute to acuminate apices, serrate or serrulate margins (the veins ending in apiculate teeth), and rounded, cuneate, or attenuate bases; surfaces of the blades usually densely stellate-pubescent when young, sometimes becoming glabrous. Flowers usually drooping on slender pedicels, solitary, in fascicles of 2–8 flowers, or in short irregular racemes; fascicles or racemes occurring above leaf scars on second-year branchlets. Calyx tube 4- or rarely 5-toothed or subentire, the tube ± completely adnate to the ovary; pedicel articulated at the base of the calyx. Corolla expanding prior to anthesis, initially greenish, becoming white to pale pink, campanulate, 4- or rarely 5-lobed or deeply cleft nearly to the base. Stamens 8–16, included or exserted, the filaments coherent basally for part of their length and adnate to the corolla. Gynoecium 2–4-carpellate; ovary ± completely inferior, 2–4-locular, each locule with 4 ovules on axile placentae; style simple, slender, terminating in a minute, sometimes 4-lobed stigma. Fruits dry, glabrous, and indehiscent, clavate, oblong, or ± ellipsoidal, prominently 2- or 4-winged, terminated by the persistent style base. Seeds 1–4 per fruit, solitary in each locule through abortion, surrounded by a stony covering. (*Mohria* Britton, non Swartz; *Mohrodendron* Britton; *Carlo-*

[2] This treatment is adapted from that of E. W. Chester, 1966.

mohria Greene.) TYPE SPECIES: *H. carolina* L. (Name honoring Stephen Hales, 1677–1761, English botanist and author of *Vegetable Staticks*, an early treatise on plant physiology.) — SILVERBELL-TREE, SNOWDROP-TREE.

Three species of the southeastern United States, one comprised of two varieties, and *Halesia macgregorii* Chun of southeastern China. With the exception of *H. macgregorii*, all the species are known in cultivation.

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KEY TO THE SPECIES OF HALESIA IN CULTIVATION

1. Corolla shallowly 4-(5-)lobed, the lobes less than ½ the length of the campanulate corolla (or rarely cleft nearly to the base); stamens 8–16; fruits 4-winged; leaves generally 2 times or more longer than broad. . . . . 2.
2. Stamens exserted from the corolla at anthesis; corolla 8–15 mm. long; fruits clavate, narrowly tapered to the base. . . . . 1. *H. parviflora.*
2. Stamens included within the corolla at anthesis; corolla 13–22 mm. long; fruits ellipsoidal with broad, rounded bases, rarely ± clavate. . . . . 2. *H. carolina.*

1. Corolla deeply cleft almost to the base into 4 (or 5) petal-like lobes; stamens usually 8, rarely to 16; fruits broadly 2-winged; leaves generally less than 2 times as long as broad. . . . . 3. *H. diptera.*

1. **H. parviflora** Michaux, Fl. Bor.-Am. 2: 40. 1803. FIGURE 1, d–f.

Shrubs or small trees to ca. 10 m., with dark, blackish-brown bark fissured into narrow ridges; branchlets reddish-brown, obscurely stellate-pubescent, becoming glabrous. Petioles 0.5–1.9 cm. long; leaf blades oblong-ovate to elliptic, 6–17 cm. long, 2.5–8 cm. wide, with acute to acuminate apices, serrulate margins, and cuneate to rounded bases; upper and lower surfaces whitened by stellate hairs when young, at maturity dull green, pubescent or glabrous above, finely stellate-pubescent below, particularly along the primary veins. Flowers long-pedicellate, appearing in spring with the leaves, usually 3 or 4 together in fascicles or occasionally in irregular short racemes; pedicels and calyces 6–15 mm. long, the calyx tube subentire or 4-toothed; corolla white, campanulate, shallowly 4-lobed, 8–15 mm. long; stamens 8–16, equal, exserted from the corolla at anthesis; style elongate, exserted, usually exceeding the stamens; ovary inferior, 2–4-loculate. Fruits clavate, terminated by the persistent style base, gradually narrowed to the base, 2–4 cm. long, with 4 narrow, ± equal wings. $2n = 24$. (*Halesia tetraptera* L. var. *parviflora* (Michx.) Schelle; *H. tetraptera* Ellis, *sensu* Godfrey; *Mohrodendron parviflorum* (Michx.) Britton.) — LITTLE SILVERBELL, FLORIDA SILVERBELL.

Native to the Coastal Plain of the southeastern United States in South Carolina, Georgia, northern Florida, Alabama, and Mississippi.

2. **H. carolina** Linnaeus, Syst. Nat. ed. 10. 1044. 1759. FIGURE 1, a–c.

Small trees, often with several trunks from near the base, to 10 m., or occasionally large trees with a single trunk to 30 m.; bark bluish-gray with longitudinal whitish or buff-colored streaks, becoming rough and ridged in old specimens; branchlets with blackish bark exfoliating in thin, longitudinal strips. Petioles stout, 0.7–2.4 cm. long; leaf blades ovate to ovate-oblong, 9.5–22.5 cm. long, 4.5–9.8 cm. wide, with acute, short- or long-acuminate apices, finely serrulate margins, and cuneate to rounded bases; blades finely and often densely stellate-pubescent when young, at maturity bright green and puberulous above, pale green, glabrous or finely stellate-pubescent, particularly along the veins, below. Flowers borne on slender, drooping pedicels, appearing in spring with expanding leaves, in 3–8-flowered fascicles, in short, congested racemes, or rarely solitary; pedicels and calyces 1–2.3 cm. long, the calyx tube obconic, with 4 deltoid or obsolete lobes; corolla white, white flushed with pink, or pink, campanulate, 1.3–2.2 cm. long, with 4 shallow lobes (or rarely cleft to below the middle); stamens 8–16, equal, included within the corolla; ovary inferior, 4-locular, the slender style included or exserted. Fruits green, becoming reddish-brown, usually ellipsoidal, terminated by the persistent style base, rounded or tapered slightly at base, 2–6 cm. long, with 4 broad to narrow wings. $2n = 24$. (*Halesia tetraptera* Ellis; *H. tetraptera* L.; *Mohrodendron carolinum* (L.) Britton; including *H. tetraptera* f. *meehanii* Meehan ex Sarg., *H. carolina* f. *dialypetala* (Rehder)

Schneider, *H. carolina* var. *mollis* (Lange) Perkins, *H. monticola* (Rehder) Sarg., *H. monticola* var. *vestita* Sarg., and *H. monticola* var. *vestita* f. *rosea* Sarg.) — SILVERBELL-TREE, SNOWDROP-TREE.

Native to the southeastern United States from West Virginia and Virginia south to South Carolina and northern Alabama, and westward through Kentucky, Tennessee, and southern Ohio to Illinois, Arkansas, and Oklahoma.

Variable in habit (small, shrublike trees, often with several trunks from the base, to large, single-trunked trees), flower size and color (white, white flushed with pink, or pinkish throughout), and leaf size and pubescence, *Halesia carolina* has been treated as comprised of several varieties or has been divided into two closely related species, each with a number of subordinate taxa. The majority of these taxa, moreover, have been recognized at one time or another by botanists, horticulturists, and nurserymen, resulting in a confused and awkward taxonomy. Recent studies by Chester (1966), however, show that the characters used to define these taxa (regardless of the rank assigned to them) are either clinal over portions of the geographic range of the complex or exhibit random variation without correlations worthy of taxonomic recognition. As a result, *H. carolina* is treated here as a single, variable species without a constellation of varieties or forms.

Two names placed in synonymy have previously been considered as cultivars. Forma *meehanii* Meehan ex Sarg. (Gard. Forest **5**: 534. 1892) (*H. carolina* L. var. *meehanii* (Meehan ex Sarg.) Perkins, Pflanzenr. IV. **241**(30): 97. 1907) (= cv. Meehanii), a small bushy tree, was described from a plant that appeared as a seedling. Chester considers this plant to be a teratological form of *H. carolina* with short-pedicellate flowers, small, cup-shaped corollas, and thickish, rugose leaves. In addition, plants of *H. monticola* var. *vestita* Sarg. (Jour. Arnold Arb. **2**: 171. 1921) with pink flowers have been designated as f. *rosea* Sarg. (*loc. cit.*) (= cv. Rosea) and have also been considered as a cultivar of *H. carolina*. It should be noted, however, that evidence presented by Chester indicates that the pink coloration of the corollas is subject to environmental modification (the pink color is developed in the absence of direct sunlight) and is also partially a function of the age of the flower. It is questionable, therefore, whether corolla color would remain true unless clonal progeny were grown under certain environmental conditions.

3. **H. diptera** Ellis, Phil. Trans. Roy. Soc. London **51**: 931, 932. *t. 22, fig. b.* 1761. FIGURE 1, g, h.

Shrubs or small trees to 10 m.; bark reddish-brown, flaking into small, thin scales and irregularly longitudinally fissured; branchlets grayish or brownish, lustrous, with scattered stellate hairs, becoming glabrous and purplish-black. Petioles 1–3.3 cm. long; leaf blades ovate to obovate, 8.5–18 cm. long, 4.5–10.8 cm. wide, with acuminate apices, denticulate-serrate margins, and rounded to cuneate bases; blades light green, pubes-

cent along the veins above, pubescent over the entire surface below, particularly along the conspicuous, reticulated veins, often becoming ± glabrous with age. Flowers occurring with the leaves in spring, long-pedicellate, 2–6 together in fascicles or in short racemes; pedicels and calyces 1–1.8 cm. long, the calyx tube obconic with deltoid lobes; corolla white, 0.9–1.7 cm. long, deeply divided nearly to the base into 4 (rarely 5) ovate or obovate lobes; stamens usually 8 (or sometimes to 16), equal, included; ovary 2- or rarely 4-locular, the style elongate, slender, included. Fruits reddish-brown, compressed, oblong, terminated by the persistent style base, 2.5–5 cm. long, with 2 conspicuous broad wings. $2n = 24$. (*Mohrodendron dipterum* (Ellis) Britton.) — SNOWDROP-TREE.

Native to the Atlantic and Gulf coastal plains of the southeastern United States from South Carolina to eastern Texas.

Plants with larger flowers (the corolla 2–3 cm. long and the pedicel and calyx 1.6–2.8 cm. long) have been recognized as var. *magniflora* R. K. Godfrey (Rhodora **60**: 88. 1958). This variety occurs naturally in rich deciduous woodlands of southern Georgia, in the panhandle of northern Florida, and in southern Alabama.

2. **Pterostyrax** Siebold & Zuccarini, Fl. Jap. **1**: 94. 1839.

Deciduous trees or shrubs, the branchlets with continuous pith; winter buds enclosed by 2 overlapping, stellate-pubescent scales. Leaves petiolate, the blades chartaceous, elliptic, ovate, or oblanceolate, with entire to serrate or denticulate margins (the veins ending in apiculate teeth), attenuate to rounded bases, and acute, short-acuminate, or truncate and 3-lobed apices; upper surfaces variously pubescent, sometimes glabrescent; lower surfaces stellate-pubescent, occasionally with simple hairs along the veins. Flowers several to numerous, ± secund in densely stellate-pubescent paniculate or corymbiform inflorescences terminating short lateral branchlets from second-year wood; pedicels articulated at the base of the calyx. Calyx adnate to the ovary, with 5 teeth or lobes. Corolla white, deeply cleft almost to the base into 5 lobes. Stamens 10, exserted, the filaments connate basally for a portion of their length. Gynoecium 3-, rarely 4- or 5-carpellate; ovary inferior, 3- (4- or 5-)locular, each locule with 4 ovules; style simple, exserted, with a small, persistent annular disc at its base. Fruits indehiscent, subglobose to clavate, winged or ribbed, variously pubescent. Seeds 1 or 2, tightly enclosed in the fruit. (Including *Decavenia* Koidzumi.) TYPE SPECIES: *P. corymbosa* Sieb. & Zucc. (Name from Greek *pteron*, wing, and *Styrax*, the closely allied genus, in reference to the winged fruits of the type species.)

Four or five species of eastern Asia in Japan, China, and Burma. In addition to the two species treated below, *Pterostyrax psilophyllus* Diels and *P. leveillii* Chun have been described from China, while *P. burmanicus* Smith & Farrer is native to Burma.

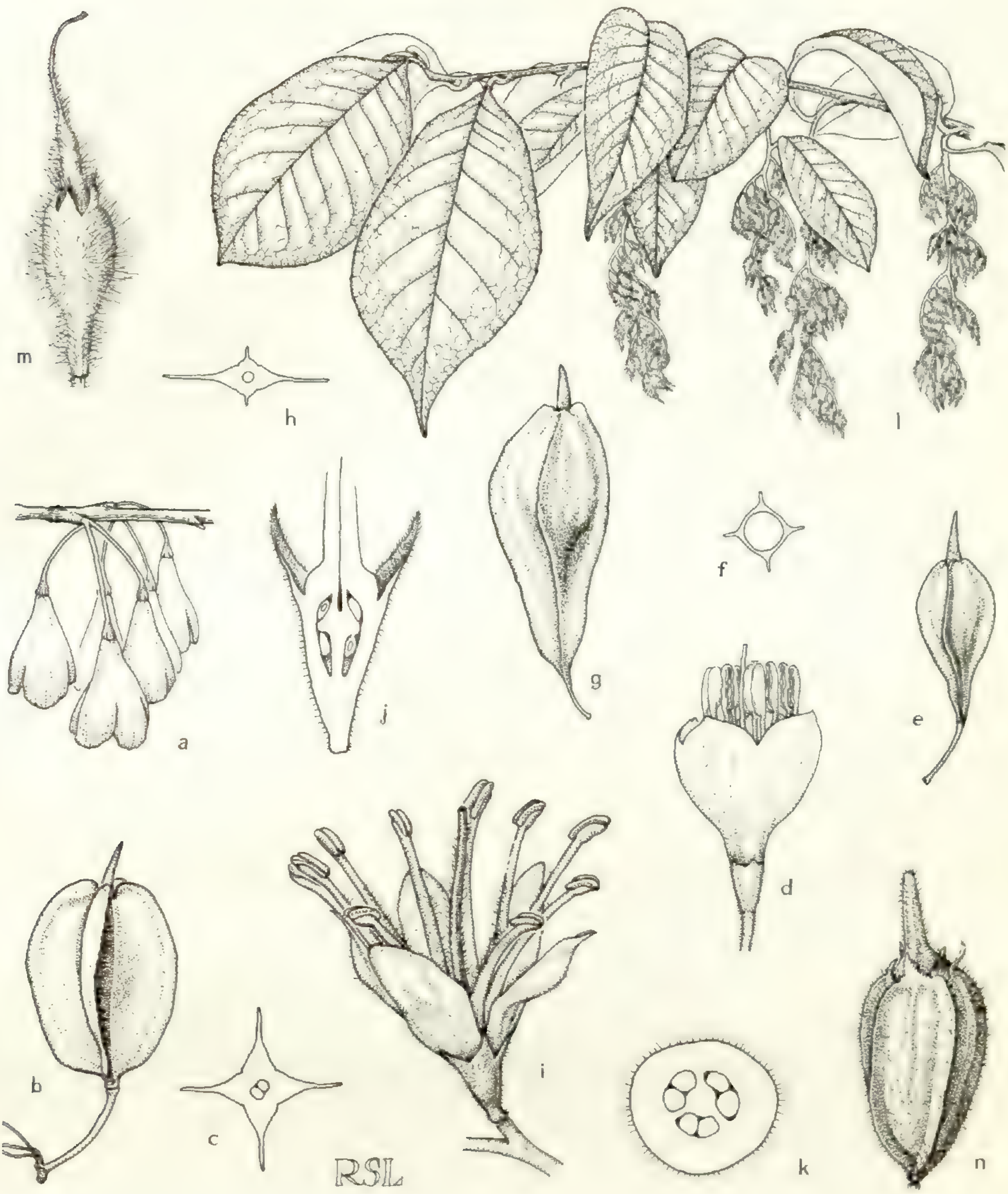

FIGURE 1. **Halesia** and **Pterostyrax.** a–h, *Halesia.* a–c, *H. carolina*: a, habit, showing fascicles of flowers, × ¾; b, four-winged fruit, × ¾; c, cross-section of fruit, showing the four ± equal wings, × ¾. d–f, *H. parviflora*: d, flower at anthesis, showing stamens exserted from the corolla, × 1½; e, pyriform, four-winged fruit, × ¾; f, cross-section of fruit, showing the four ± equal wings, × ¾. g, h, *H. diptera*: g, fruit, showing the two large wings, × ¾; h, fruit in cross-section, showing the two large and 2 small wings, × ¾. i–n, *Pterostyrax.* i–m, *P. hispida*: i, flower at anthesis, note articulation at base of calyx, × 3; j, longitudinal section of flower (corolla and androecium removed), × 6; k, cross-section of ovary, showing 3-locular condition, × 12; l, habit, showing pendent infructescences, × ¼; m, individual fruit, showing long, bristlelike hairs, × 3. n, fruit of *P. corymbosa*, × 3.

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COBB, A. J. The flower garden. Gard. Chron. III. **58:** 6, 7. 1915. [Short notes concerning *Pterostyrax* also appear in the following issues of the Gardeners' Chronicle: **46:** 88. *fig. 37.* 1909; **48:** 123, 125. 1910; **131:** 218. *fig. 97.* 1952.]

FANG, W. P. *Pterostyrax hispidus* Siebold & Zuccarini. Icones Pl. Omeiensium **1**(1): *pl. 50.* 1942.

NASH, G. V. *Pterostyrax hispida.* Addisonia **5:** 59, 60. *pl. 190.* 1921.

SHIRASAWA, H. *Halesia hispida* and *Halesia corymbosa.* Icones Essences Forestières Jap. **2:** *t. 65.* 1908.

KEY TO PTEROSTYRAX HISPIDA AND PTEROSTYRAX CORYMBOSA

1. Flowers in pendent, secund, paniculate inflorescences (8–)10–20 cm. long; calyx lobes deltoid; lower surfaces of the leaf blades stellate-pubescent, usually with long, simple hairs along the veins; young branchlets glabrous; fruits finely ribbed, stellate-pubescent and beset with longer, stiff, yellowish-brown simple hairs. ..... 1. *P. hispida.*
1. Flowers in drooping, ± secund, corymbiform inflorescences 6–8 cm. long; calyx lobes subulate; lower surfaces of the leaf blades stellate-pubescent, without simple hairs along the veins; young branchlets loosely stellate-pubescent; fruits 5-winged, finely stellate-pubescent, lacking long, simple hairs. ..... 2. *P. corymbosa.*

1. **P. hispida** Siebold & Zuccarini, Abh. Math-Phys. Cl. Akad. Wiss. München **4**(3): 132. 1846; Fl. Jap. Fam. Nat. **2:** 8. 1846.

FIGURE 1, i–m.

Trees or shrubs, often with several trunks from the base, to ca. 14 m., with brownish or grayish bark fissured in a checkered pattern; young branchlets reddish-brown, glabrous, the periderm on older growth exfoliating in thin strips. Leaf blades 7–14 cm. long, 2.5–6.5 cm. wide, oblong, obovate, or lanceolate, with attenuate bases, finely denticulate margins, and acute to attenuate apices; upper surfaces bright green with scattered simple hairs, particularly along the veins, becoming glabrous; lower surfaces pale, grayish-green, sparsely to densely stellate-pubescent over the entire surface and with simple hairs along the veins. Flowers secund in pendent paniculate inflorescences (8–)10–20 cm. long terminating short, lateral branchlets, often with reduced paniculate inflorescences in the axils of the subtending leaves; pedicels and calyces 4–5 mm. long, densely stellate-pubescent, the calyx lobes ± deltoid; corolla lobes 6–7 mm. long, linear-oblong, densely stellate-pubescent; stamens long-exserted, the filaments free nearly to the base; style exserted, exceeding the stamens. Infructescences pendent, the fruits (8–)10–15 mm. long, clavate, terminated by the persistent calyx lobes and style base; surface of the fruits finely ribbed, the ribs often obscured by fine stellate hairs and numerous long, stiff, yellowish-brown simple hairs. (*P. micrantha* Sieb. & Zucc.; *Decavenia hispida* (Sieb. & Zucc.) Koidzumi; *D. micrantha* (Sieb. & Zucc.) Koidzumi.) — EPAULETTE TREE.

Native to mountainous regions of Japan; also known from Hupeh and Szechwan provinces, China. With the exception of one collection, all herbarium sheets of cultivated *Pterostyrax* from North America examined during this investigation belong to this species. A handsome small tree or large shrub that blooms during June and July, *P. hispida* deserves to be more widely planted.

2. **P. corymbosa** Siebold & Zuccarini, Fl. Jap. 1: 96. *t. 47*. 1839.

FIGURE 1, n.

Shrubs or small trees with smooth, grayish bark; young branchlets with scattered stellate hairs, the periderm on older branchlets grayish-brown, exfoliating in thin strips. Leaf blades 4–9.5 cm. wide, 6–17 cm. long, ovate or obovate to broadly elliptic or oblanceolate, with rounded to attenuate bases, subentire, serrulate, or denticulate margins, and short-acuminate apices; upper surfaces pale green, finely stellate-pubescent, particularly along the veins, the lower surfaces with scattered stellate hairs. Flowers in short, drooping, ± secund, corymbiform inflorescences 6–8 cm. long, terminating short, lateral branchlets, sometimes with small inflorescences in the axils of subtending leaves; pedicels and calyces 3–4 mm. long, densely stellate-pubescent, the calyx lobes subulate; corolla lobes 7–8 mm. long, linear-elliptic, densely stellate-pubescent; stamens exserted, the filaments connate, often forming a tube for most of their length; style exserted, about as long as or longer than the stamens. Infructescences drooping, the fruits 10–17 mm. long, narrowly 5-winged, terminated by the persistent basal portion of the style; surfaces of the fruits very finely stellate-pubescent. $2n = 24$. (*Halesia corymbosa* (Sieb. & Zucc.) Nicholson.)

Native to mountainous regions of Japan and Kiangsi and Hunan provinces, China; to our knowledge, documented as cultivated in North America by only one collection (*F. G. Meyer 13808*, May 12, 1973, AAH, NA) from a private garden in Maryland.

3. **Rehderodendron** H. H. Hu, Bull. Fan Mem. Inst. Biol. 3: 77. *pls. 1, 2*. 1932.

Deciduous trees (and shrubs?), the branchlets with continuous pith; winter buds ovoid, with 2 or 3 finely stellate-pubescent outer scales. Leaves petiolate, the blades chartaceous to coriaceous, elliptic to oblong-ovate, with acute to acuminate apices, serrate or serrulate margins (the veins ending in apiculate teeth), and attenuate to ± rounded bases; surfaces of the blades glabrous, glabrescent, or densely stellate-pubescent, particularly along the veins. Flowers borne on slender pedicels in leafless racemose or paniculate inflorescences above leaf scars on second-year branchlets. Calyx tube obconic, 5-toothed, the tube adnate to the ovary. Corolla white, occasionally flushed with pink, deeply 5-lobed nearly to the base. Stamens (8–)10, of 2 lengths, the filaments coherent at the

base and often adnate to the corolla or free. Gynoecium 3–5-carpellate; ovary ± totally inferior, 3–5-locular, each locule with 4–6 ovules; styles simple, slender. Fruits large and woody, with thin, corklike exocarp and fibrous, spongy endocarp, indehiscent, glabrous or stellate-pubescent, oblong or ellipsoidal, unribbed and smooth or ribbed and sometimes deeply sculptured. Seeds 1–3, cylindric. LECTOTYPE SPECIES: *R. macrocarpum* H. H. Hu; see H. H. Hu, Lingnan Sci. Jour. 12(suppl.): 112. 1933. (Name honoring Professor Alfred Rehder, Curator of the Arnold Arboretum, student of Chinese botany, and teacher of Chinese botanists, and from Greek *dendron*, tree.)

Perhaps ten species of eastern Asia in the temperate and subtropical regions of China and Indo-China. Although ten species have been described, it is doubtful that all would be maintained if the taxonomy of the genus were re-evaluated. Poorly represented in herbarium collections, the genus is infrequently encountered in cultivation; only the lectotype species is documented as grown in North America.

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1. R. macrocarpum H. H. Hu, Bull. Fan Mem. Inst. Biol. 3: 78. *pl. 1.* 1932. FIGURE 2, a–d.

Small trees to ca. 10 m. with grayish-black bark; young branchlets reddish-brown, glabrescent, the buds stellate-pubescent. Leaves membranaceous, 7–13 cm. long, 3.5–5.5 cm. wide, elliptic-ovate to oblong or lanceolate, with acute to acuminate apices, serrulate, red-tinged margins, and broadly cuneate to subrounded bases, the lamina sometimes decurrent along the short, glabrescent, scarlet petiole; upper surfaces green or reddish-green, glabrous, the lower surfaces paler green and stellate-pubescent along the reddish midvein and primary veins. Flowers borne on slender pedicels 3–10(–15) mm. long in short, few-flowered paniculate inflorescences; calyx tube ca. 4 mm. long, the lobes deltoid; corolla white (or apparently sometimes flushed with pink), the 5 lobes 10–15(–18) mm. long, ovate to elliptic, pubescent on both surfaces; stamens (8–)10, of 2 lengths, partly exserted; ovary inferior, the simple style about equalling the longer stamens. Fruits oblong-ovoidal, light reddish-brown, (4–)6–8.5 cm. long, 2.5–3 cm. in diameter, 8–10 ribbed, glabrous; seeds 1 or 2 through abortion, cylindrical, brown, ca. 5 cm. long.

Apparently endemic to a small area of Szechwan Province in western China, where the original collections of this species were made on Mount Omei between 1800 and 2000 meters.

4. **Styrax** Linnaeus, Sp. Pl. 1 : 444. 1753; Gen. Pl. ed. 5. 203. 1754.

Evergreen or deciduous trees or shrubs, usually with several superposed winter buds with 1 outer scale; young branchlets commonly stellate-pubescent. Leaves subsessile to distinctly short-petiolate, the blades ovate, elliptic, oblong, lanceolate, or occasionally suborbicular, with subentire, serrate, dentate, or lobulate margins; surfaces of the blades glabrous or variously stellate-pubescent. Flowers arranged in axillary and/or terminal paniculate, racemose, or corymbose inflorescences, usually on short lateral branchlets and often with solitary or 2 to several flowers in the axils of subtending leaves. Calyx persistent, cuplike, 5- or rarely 6- or 7-

FIGURE 2. **Rehderodendron** and **Styrax.** a–d, *Rehderodendron macrocarpum*: a, habit of paniculate inflorescences on a second-year branchlet, × ½; b, flower (corolla and some stamens removed) showing stamens of two unequal lengths and articulation at base of calyx, × 2; c, woody, ribbed fruit, × ½; d, cross-section of fruit showing two seeds and fibrous endocarp, × ¾. e, habit of leafy raceme of *Styrax americana*, × ½. f, g, *S. obassia*: f, flower (note lack of articulation at base of calyx), × ¾; g, longitudinal section of flower showing perigynous insertion of the corolla and epipetalous filaments, × 6. h, i, *S. japonica*: h, habit, showing pendulous fruits, × ½; i, seed, showing conspicuous basilateral hilum, × 2.

toothed, undulate, or subentire. Corolla usually white, sometimes reddish-brown on the adaxial surface, deeply to shallowly cleft into 5 (rarely 6 or 7) lobes, the corolla tube shorter or rarely longer than the free lobes, insertion hypogynous to perigynous; corolla lobes imbricate or valvate in bud, often stellate-pubescent on the abaxial surfaces, usually spreading or reflexed at anthesis. Stamens 10, the filaments basally connate and adnate to the corolla tube. Gynoecium 3-carpellate; ovary essentially superior to partially inferior, usually adnate to the calyx tube, at least basally, 1–3-locular at base, 1-locular above, with 4–6 ovules per locule; style simple, elongate, terminated by a small, often 3-lobed, capitate stigma. Fruits dry, crustaceous, subtended by the persistent calyx, globose to ovoid-oblong, apically 3-valvate, irregularly dehiscent, or indehiscent. Seeds 1 or rarely 2, subglobose, ovoid, or ellipsoidal, with a conspicuous basilateral hilum, the seed coat hard and smooth, crustaceous, wrinkled, papillate, or stellate-pubescent. TYPE SPECIES: *S. officinale* L. (*Styrax*, the Greek name for the type species and for storax, a resin obtained from that species and used in incense.) — STYRAX, SNOWBELL.

Approximately 120 species of eastern Asia (primarily in tropical and subtropical areas), the West Indies, South and Central America, the Mediterranean region (one species), and North America, where about six species are native. Several species native to the East Indies (not in cultivation in our area) are the sources of the resin benzoin, which is used medicinally as an expectorant, stimulant, and antiseptic, as well as in the manufacture of perfumes and vanilla cream candies. Often termed storax, the resin obtained from species of *Styrax* should not be confused with resins derived from species of *Liquidambar* (Hamamelidaceae), which are known as styrax.

Styrax shirianum Makino of Japan and *S. veitchiorum* Hemsley & Wilson of China were included by Rehder (1940, 1949) but are omitted from the present treatment, since we have found no evidence of their cultivation in our area. Both of these species are grown in England and are attractive ornamentals worthy of cultivation in North America. Moreover, *S. suberifolium* Hooker & Arnott, an evergreen species of China and Taiwan, has been incorrectly recorded as growing at the United States National Arboretum; it is therefore not included here.

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KEY TO THE SPECIES OF STYRAX IN CULTIVATION

1. Inflorescences terminal, few-flowered leafy racemes, the flowers paired (or rarely solitary) terminally, and usually solitary or paired in the axils of subtending leaves. ..... 1. *S. americanum.*
1. Inflorescences few to many-flowered, bracteate, terminal and/or axillary racemes or panicles, often with solitary or fascicled flowers in the axils of subtending leaves. ..... 2.
2. Pedicel and calyx glabrous, 2.5–3.5 cm. long; corolla lobes ± ovate, 6–8 mm. wide. ..... 2. *S. japonicum.*
2. Pedicel and calyx stellate-pubescent (rarely glabrous), up to 1.8 cm. long; corolla lobes elliptic to ovate, up to, or rarely exceeding, 7 mm. in width. ..... 3.
3. Lower surfaces of the leaf blades densely matted, felted or entirely covered with stellate hairs, the hairs sometimes minute. ... 4.
4. Lateral and terminal buds concealed by petiole bases; flowers in terminal racemes (7–)12–17 cm. long, often with solitary flowers in the axils of subtending leaves; corolla lobes (1.3–)1.5–2 cm. long. ..... 4. *S. obassia.*
4. Lateral and terminal buds exposed, not concealed by petiole bases; flowers in terminal and/or axillary racemes or panicles less than 10 cm. long, often with solitary or fascicled flowers in the axils of leaves below; corolla lobes less than 1.5 cm. long. ..... 5.
5. Leaf blades (1–)1.5–3(–4) cm. long, (0.5–)1.5–2(–2.5) cm. wide, the majority with irregularly and shallowly lobulate margins above the middle, entire or serrulate below the middle. ..... 8. *S. wilsonii.*
5. Leaf blades (4–)5–11(–16) cm. long, 2–10(–11) cm. wide, the margins entire, serrate, undulate to angulate or occasionally sinuately lobulate. ..... 6.
6. Leaves usually suborbicular to broadly ovate, the margins undulate to angulate and often sinuately lobulate. ..... 7. *S. platanifolium* var. *platanifolium.*
6. Leaves usually elliptic to obovate, the margins entire or serrate. ..... 7.
7. Flowers alternate or paired in inconspicuously bracteate racemes terminating short lateral branchlets, often with smaller axillary racemes or solitary or paired flowers in the axils of leaves below; filaments ± dense-

ly stellate-pubescent at base; petioles (3–)5–10 mm. long. ..... 3. *S. grandifolium.*

7. Flowers fascicled as well as occasionally solitary and alternate in bracteate axillary and/or terminal panicles, often with fascicled flowers in the axils of subtending leaves; filaments densely villous at base; petioles 1–3 mm. long. ..... 6. *S. dasyanthum* var. *cinerascens.*

3. Lower surfaces of the leaf blades glabrous or with scattered stellate hairs, primarily along the veins, the surfaces not densely matted, felted or entirely covered by stellate hairs. ..... 8.

8. Flowers in few-flowered axillary racemes (at anthesis the flowers often appearing fasciculate and the racemes terminal); leaves with undulate to angulate and often sinuately lobulate margins. ..... 7. *S. platanifolium* var. *stellatum.*

8. Flowers in several- to many-flowered terminal and/or axillary racemes or panicles, often with solitary or fascicled flowers in the axils of subtending leaves; leaves with subentire, serrate, or denticulate margins. ..... 9.

9. Filaments densely villous at base; petioles 1–3 mm. long; flowers fascicled as well as occasionally solitary and alternate in bracteate axillary and/or terminal panicles, often with fascicled flowers in the axils of subtending leaves. ..... 6. *S. dasyanthum* var. *dasyanthum.*

9. Filaments stellate-pubescent at base; petioles (3–)5–15 mm. long; flowers alternate or paired in inconspicuously bracteate, sometimes basally branched, terminal racemes, often with smaller axillary racemes or solitary or paired flowers in the axils of leaves below. ..... 10.

10. Small trees; calyx densely rusty stellate-pubescent; terminal racemes usually branched basally; raceme rachis subglabrous to finely stellate-pubescent. ..... 5. *S. hemsleyanum.*

10. Shrubs; calyx densely silvery stellate-pubescent; terminal racemes usually simple; raceme rachis densely stellate-pubescent. ..... 3. *S. grandifolium.*

1. **S. americanum** Lamarck, Encycl. Méth. Bot. **1**: 82. 1783.

FIGURE 2, e.

Shrubs to 4 m.; young branchlets sparingly stellate-pubescent, becoming glabrous; periderm on older branchlets exfoliating in thin strips, exposing dark, purplish-black or silvery-gray bark. Leaves short-petiolate, the petioles (1–)3–5 mm. long; leaf blades elliptic, oblong, or ovate to obovate, 2–10 cm. long, 1.5–3.5 cm. wide, with acute to short-acuminate apices, obscurely to distinctly serrate margins, and acute bases; upper surfaces of the blades dark green, glabrous to sparingly stellate-pubescent, the lower surfaces pale green, glabrous to densely stellate-pubescent. Flowers in short, few-flowered, leafy racemes, the flowers solitary or usually paired terminally at the ends of short branchlets and solitary or paired in the axils of leaves below; pedicels drooping, slender, the pedicels and

calyces glabrous to densely stellate-pubescent, (7–)9–18 mm. long; corolla lobes oblong-elliptic, 10–12 mm. long, 3–5 mm. wide; stamens included, the styles slightly exserted. Fruits apically 3-valvate, subglobose, 8–10 mm. long, tan; seeds dull reddish-brown, longitudinally grooved, subglobose, 8–10 mm. long, usually 1 per fruit. $2n = 16$. (Including *S. americanum* var. *pulverulentum* (Michx.) Rehder.)

Native to the eastern United States from Pennsylvania southward into Florida and west into Indiana, Illinois, Missouri, Arkansas, and eastern Texas. Both Rehder (1940, 1949) and Gonsoulin (1974) recognized plants with elliptic to ovate or obovate leaves, the petioles and upper surfaces of the blades sparingly stellate-pubescent and the lower surfaces of the blades pulverulent and finely to densely stellate-pubescent, and with densely stellate-pubescent pedicels and calyces as var. *pulverulentum* (Michx.) Rehder in Bailey (Stand. Cyclop. Hort. 6: 3280. 1917) (*S. pulverulentum* Michx., *S. americanum* f. *pulverulentum* (Michx.) Perkins). However, the numerous plants intermediate between var. *americanum* and var. *pulverulentum* attest to Gonsoulin's report (1974) that hybridization and backcrossing occur in localities where the two taxa grow together, and they indicate that recognition of var. *pulverulentum* is not merited.

2. **S. japonicum** Siebold & Zuccarini, Fl. Jap. 1: 53. *t. 23*. 1835.
FIGURE 2, h, i.

Shrubs or many-branched small trees to 10 m.; young branchlets glabrate, older branchlets with silvery-gray periderm exfoliating in thin strips, exposing reddish- or purplish-brown inner bark. Leaves petiolate, ± erect or ascending, the blades elliptic-ovate to narrowly oblong, 2.5–8(–12) cm. long, 1.5–3.5(–6.5) cm. wide, with acute, abruptly acuminate, or short-caudate apices (the apex itself often mucronulate), finely serrulate margins (often entire below the middle), and cuneate to attenuate bases, the lamina often decurrent along the sparingly pubescent petiole; upper and lower surfaces of the blades with scattered stellate hairs, principally along the veins. Flowers pendulous, in loose, 3–5-flowered racemes terminating short lateral branchlets, usually with solitary flowers in the axils of subtending leaves; pedicels long and slender, the pedicels and calyces 2.5–3.5 cm. long, glabrous; corolla lobes 9–14 mm. long, 6–8 mm. wide, ovate-elliptic; stamens slightly shorter than the corolla; styles ± exserted. Fruits subglobose to ellipsoidal, often with a mucronate apex, (9–)10–15 mm. long; seeds 1 or rarely 2 per fruit, ovoidal, reddish-brown, longitudinally 2- or 3-grooved. $2n = 40$. — JAPANESE SNOWBELL.

Native to Japan, China, Korea, Taiwan, and the Philippines. Several varieties and forms, some of questionable validity, have been recognized from over the geographic range of the species, yet none of these variants appear to be in cultivation in our area. This is undoubtedly the most frequently encountered cultivated species of *Styrax*.

3. **S. grandifolium** Aiton, Hort. Kew. 2: 75. 1789.

Shrubs to about 8 m.; young branchlets finely roughened by stellate hairs, the older branchlets with blackish or brownish, finely fissured bark. Leaves petiolate, the petioles (3–)5–11 mm. long; leaf blades elliptic to ovate or typically obovate, 4–10(–20) cm. long, 2.5–7(–12) cm. wide, with short-acuminate or acute apices, subentire or remotely serrulate or denticulate margins, and cuneate to subrounded bases; upper surfaces of the blades pale to dark green, with minute stellate hairs along the veins when young; lower surfaces of the blades glabrous or usually sparsely to densely stellate-pubescent over the entire surface, the pubescence often imparting a silvery- or grayish-green color. Flowers in terminal, bracteate racemes 5–10 cm. long on short lateral branchlets, usually with paired or solitary flowers, or occasionally smaller racemes in the axils of subtending leaves; pedicels and calyces 8–11 mm. long, silvery stellate-pubescent; corolla lobes 10–14 mm. long, 3–4 mm. wide; stamens ± as long as the corolla, the filaments densely stellate-pubescent at base; styles ± exserted. Fruits globose, often with an apiculate apex, 7–9 mm. in diameter, apically 3-valvate; seeds 1 or rarely 2 per fruit, subglobose, 7–9 mm. long, dull dark brown. $2n = 32$. — BIG-LEAF SNOWBELL.

Native to the southeastern United States from Virginia and Tennessee southward into Florida, Alabama, Mississippi, Louisiana, and eastern Texas. Plants of *Styrax grandifolium* have been reported to sucker extensively from the roots.

4. **S. obassia** Siebold & Zuccarini, Fl. Jap. 1: 93. *t. 46.* 1835.

FIGURE 2, f, g.

Shrubs or more often small trees to 10 m. with ascending to horizontal branches, usually forming a rounded crown; young branchlets floccose stellate-pubescent, soon glabrous, the periderm on second-year branchlets dark reddish-brown or blackish, exfoliating in thin sheets. Petioles floccose stellate-pubescent, becoming glabrous, the lower portion winged, enclosing the terminal or lateral buds; leaf blades broadly elliptic or more commonly suborbicular or orbicular, 8–16(–20) cm. long, 8–14 cm. wide, with shortly acuminate to rounded apices, subentire to irregularly dentate margins (the teeth apiculate), and rounded to broadly cuneate or truncate bases; upper surfaces of the blades dark green, with stellate hairs along the veins, becoming glabrous; lower surfaces of the blades grayish-green, densely matted with stellate hairs, when young with floccose stellate hairs along the veins. Flowers in drooping terminal racemes (7–)12–17 cm. long on short lateral branchlets, often solitary in the axils of leaves below; pedicels and calyces 1.2–2 cm. long; corolla lobes (1.3–)1.5–2 cm. long, 5–9 mm. wide, elliptic to elliptic-ovate; stamens about as long as the corolla, the styles slightly longer. Fruits (1–)1.5–2 cm. long, subovoid to conical, often with a short, rostrate apex, the surface

longitudinally wrinkled, grayish- or greenish-white; seeds 1 per fruit, ± ovoid, ca. 1.5 cm. long, dull reddish-brown. $2n = 16$.

Native to Japan, China, Korea, and Manchuria. The beautiful large racemes, often partially hidden by the large leaves, and the handsome habit of the plants make this species deserving of wider use as an ornamental.

5. **S. hemsleyanum** Diels, Bot. Jahrb. **29**: 530. 1901.

Trees (or shrubs?) to ca. 10 m., young branchlets sparingly stellate-pubescent, soon glabrous, the periderm on older branchlets exfoliating in thin, longitudinal strips, exposing grayish- or reddish-brown inner bark. Leaves petiolate, the blades ovate, obovate, broadly elliptical, or lanceolate, 6–10.5(–13) cm. long, 2.5–6.5(–9) cm. wide, with remotely serrulate to finely serrate or denticulate margins, abruptly acuminate (or rarely rounded) apices, and broadly cuneate to rounded bases; lower surfaces of the blades reticulate, glabrate, or with scattered stellate hairs along the veins. Flowers in remotely bracteate terminal racemes on short lateral branchlets, the racemes (4–)6–13.5 cm. long, often branched below and often with smaller racemes in the axils of subtending leaves; pedicels and calyces 0.8–1.2 cm. long, the calyx tubes densely stellate-pubescent and with large, darker stellate hairs scattered over the surface; corolla lobes elliptic, 0.9–1.5 cm. long, 4–5 mm. wide; stamens included, the styles ± equalling the corolla. Fruits oblong-ovoid, 1–1.3 cm. long, dehiscing into 3 valves from the apiculate apex; seeds 1 per fruit, ovoid-acute, reddish-brown, ca. 1–1.2 cm. long, the seed coat often with 1 or 2 shallow longitudinal grooves.

Native to Honan, Hupeh, and Szechwan provinces in central China.

6. **S. dasyanthum** Perkins, Bot. Jahrb. **31**: 485. 1902.

Shrubs or small trees to 8 m.; young branchlets finely stellate-pubescent, becoming glabrous, the periderm on older branchlets exfoliating in thin strips, exposing dark reddish- or purplish-brown bark. Leaves subsessile to short-petiolate, the petioles 1–3 mm. long; leaf blades elliptic, broadly elliptic, or obovate, (2–)4–13.5 cm. long, (1.5–)2–6(–7) cm. wide, with finely serrate margins, cuneate to rounded bases, and acute, acuminate, or abruptly acuminate apices; upper surfaces of the leaf blades glabrous or with scattered stellate hairs primarily along the midvein; lower surfaces of the blades with scattered stellate hairs primarily along the veins and in the axils of the midvein and lateral veins. Flowers solitary and fascicled in bracteate panicles 6–8 cm. long terminating short lateral branchlets, with solitary, paired, or fascicled flowers in the axils of subtending leaves; pedicels and calyces 8–12(–14) mm. long; corolla lobes lanceolate, (7–)9–11 mm. long, ca. 2 mm. wide; stamens ± as long as the corolla, the filaments densely villous at base; styles slightly

exserted. Fruits ovoid, 8–11(–15) mm. long, often with a rostrate apex; seeds 1 per fruit, reddish-brown, the seed coat finely wrinkled.

Native to central China. The majority of herbarium specimens of this species from cultivation in North America are referable to var. *cinerascens* Rehder (Pl. Wilsonianae 1: 289. 1912), which was based on a plant from Hupeh Province. Plants of var. *cinerascens* differ from plants of var. *dasyanthum*, described above, in the dense stellate pubescence of the young branchlets and in the matted stellate pubescence of the lower surfaces of the leaf blades.

7. **S. platanifolium** Engelmann ex Torrey, Smithsonian Contr. Knowl. 6: 4, *in nota*. 1853.

Many-branched small trees or shrubs to 4 m.; young branchlets finely or remotely stellate-pubescent, the periderm on older branchlets exfoliating in thin, longitudinal strips. Leaves petiolate, the petioles 5–10 (–13) mm. long; leaf blades suborbicular to broadly ovate, (1.5–)2.5–8 cm. long, (1.5–)2–9 cm. wide, with subcordate, rounded, truncate, or obtuse bases and undulate to angulate, often sinuately lobulate margins; upper surfaces of the leaf blades dull green, glabrous, the lower surfaces glabrous or with scattered hairs along the conspicuously reticulated veins. Flowers in short, 3–5-flowered, ± drooping, axillary racemes, the racemes often appearing terminal and the flowers often appearing fasciculate at anthesis; pedicels and calyces 8–12(–18) mm. long, glabrous or finely puberulent; corolla lobes 12–14(–15) mm. long, 4–6 mm. wide; stamens included, the style slightly exserted. Fruits globose or subglobose, 7–8 mm. in diameter, apically 3-valvate, the slender style often persistent; seeds 1 per fruit, globose, ca. 7 mm. in diameter, orangish-brown.

Endemic to limestone canyons of the Edwards Plateau of Texas. Plants with the lower surfaces of the leaf blades and the pedicels and calyces thinly to densely stellate-pubescent have been recognized as var. *stellatum* Cory (Madroño 7: 111. 1943). Although *Styrax platanifolium* is reported as cultivated at the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania, it is not known whether var. *platanifolium*, var. *stellatum*, or both are represented in the collections there.

8. **S. wilsonii** Rehder, Pl. Wilsonianae 1: 293. 1912.

Small, many-branched shrubs to ca. 2 m.; young branchlets densely stellate-pubescent, older branchlets with finely fissured, purplish-black bark. Leaves subsessile to short-petiolate, the petioles 1–3 mm. long; leaf blades broadly elliptic to rhomboid, (1–)1.5–4 cm. long, (0.5–)1.5–2.5 cm. wide, with acute to acuminate apices, irregularly and shallowly lobulate margins (often subentire below the middle), and cuneate bases; upper surfaces of the blades green, with stellate hairs along the veins, the lower surfaces grayish, densely matted with stellate hairs, often with

additional rusty stellate hairs along the veins. Flowers on very short lateral branchlets, in 3–5-flowered, bracteate, terminal racemes and occasionally in the axils of the few leaves below; pedicels and calyces 6–8 mm. long, the calyx densely stellate-pubescent, with larger rusty stellate hairs superimposed and scattered over the surface; corolla lobes 7–8 mm. long, 2–3 mm. wide, elliptic; stamens ± as long as the corolla; styles slightly exserted. Fruits subglobose, ca. 5 or 6 mm. in diameter, the subtending calyx persistently stellate-pubescent; seeds ovoid-subglobose, 5–6 mm. long, reddish-brown. (*S. wilsonii* Rolfe.)

Apparently endemic to western Szechwan Province, China.

ARNOLD ARBORETUM
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THE GENERA OF GUTTIFERAE (CLUSIACEAE) IN THE SOUTHEASTERN UNITED STATES [1]

CARROLL E. WOOD, JR., AND PRESTON ADAMS

GUTTIFERAE A. L. de Jussieu, Gen. Pl. 255. 1789, nom. cons.

Trees, shrubs, subshrubs, or perennial or annual herbs with translucent or black secretory cavities present as dots or elongate sacs; sap resinous, yellow [white or greenish] or clear and colorless. Leaves opposite, simple, entire, exstipulate. Flowers perfect or imperfect (the plants then dioecious [or polygamous]), often showy, regular, hypogynous, in simple or compound dichasia or rarely solitary. Sepals 4 or 5[–10], when 5, quincuncially imbricate (*2* outside, *2* inside, 1 in and out). Petals 4 or 5 to 9[10], yellow, flesh-colored, greenish, or pink to white, usually asymmetrical, convolute or imbricate vertically in the bud. Androecium of numerous to few stamens, filaments elongate, distinct or united at base [or throughout], staminodia present or absent; pollen usually 3-colporate. Gynoecium of [1] 2–9[–15] united carpels; styles as many as carpels, closely connate or free and divergent, or stigmas sessile; stigmas capitate or minute, or large and flat in *Clusia*; ovary superior, placentation axile, pseudoaxile, or parietal; ovules numerous to few [or one], anatropous, 2-integumented. Fruit a septicidal capsule [berry or drupe]. Seeds small [to large], the raphe inconspicuous or forming a keel, an aril present or absent; embryo straight; endosperm lacking. (Clusiaceae Lindley, Nat. Syst. ed. *2*. 74. 1836, nom. alt. cons. Including Hypericaceae A. L. de Jussieu, Gen. Pl. 254. 1789, nom. cons.; type genus: *Hypericum* L.)
TYPE GENUS: *Clusia* L.

[1] Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation, currently under Grant BMS74–21469 (Carroll E. Wood, Jr., principal investigator). This treatment follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area; supplementary information is included in brackets. References that neither author has verified are marked with an asterisk.

We are indebted to George Avery for his data on the distribution of *Clusia rosea* in the Florida Keys and to W. T. Gillis and P. B. Tomlinson for additional comments on this species as it occurs in southern Florida. The illustration of *Clusia* was drawn by Karen S. Velmure under the supervision of Kenneth R. Robertson, who noted the occurrence of polyembryony in material collected by him and C. E. Wood, Jr., in the Fairchild Tropical Garden, Miami, Florida. The illustration of *Triadenum* is the work of Rachel A. Wheeler and is based largely on materials collected by C. E. Wood, Jr. Beverly Vincent assisted with the preparation of the typescript and part of the bibliography.

A family of about 50 genera and some 900 species chiefly of the tropics and subtropics of both hemispheres. *Hypericum* L. and *Triadenum* Raf. are widely distributed in our area; *Clusia* L. reaches it only on the Florida Keys.

Engler (1925) considered the Guttiferae to comprise five subfamilies (ten tribes), with *Clusia* in subfam. Clusioideae and *Hypericum* and *Triadenum* in subfam. Hypericoideae. Melchior adopted the same classification but added a sixth subfamily to accommodate *Lorostemon* Ducke. Other authors (e.g., Lawrence, Gleason, Hutchinson, Takhtajan) have elevated subfam. Hypericoideae to the rank of family (Hypericaceae). From studies of the comparative anatomy of the Guttiferae, the Hypericaceae, and related families, Vestal found that the Guttiferae do not differ significantly from the arborescent members of the Hypericaceae. He concluded that it is a matter of opinion whether the two taxa are considered as separate families or as a single family. After an intensive investigation of the floral anatomy, Robson concluded that Engler's subfam. Hypericoideae cannot be given familial status without dismembering the Guttiferae completely and recognizing all the other subfamilies as families, a clearly undesirable course because of the close interrelationships of these subfamilies. Robson concluded further that subfam. Hypericoideae is related to subfam. Clusioideae through *Vismia* Vandelli and to subfam. Calophylloideae through *Hypericum*.

As the name Guttiferae suggests, a distinguishing characteristic of this family is the presence of secretory cavities and/or canals throughout most of the plant body. In many arborescent members these secretory receptacles are filled with a white, yellow, or greenish resinous sap. A clear resinous sap, especially noticeable in the shrubby species of sect. MYRIANDRA, is present in many species of *Hypericum*. The secretory cavities of many of the herbaceous members of *Hypericum*, especially those of sect. HYPERICUM, have a black pigment.

The Guttiferae seem to be closely related to the tribe Bonnetieae of the Theaceae, and the two families may have evolved from a common ancestral stock.

In our area the Guttiferae are of little economic importance. A few of the shrubby species of *Hypericum* have occasionally been cultivated for ornament. Fourteen species of *Hypericum* from the Old World are listed by Bailey as being in cultivation in the United States and Canada. The European *H. perforatum* L., poisonous to farm animals, is a noxious weed, especially in western North America and Australia. In the West Indies *Garcinia Mangostana* L., mangosteen, $2n = 76$, and *Mammea americana* L., mamee apple, *mamey amarillo*, *mamey de Santo Domingo*, are highly prized for their edible fruits. *Mammea* is cultivated to some extent in southern Florida. Experimental plantings of the mangosteen have been made in southern Florida, but this strictly tropical fruit has not yet been a success. Moderate success has been achieved with a few other species of *Garcinia*, including *G. Livingstonei* T. Anderson.

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KEY TO THE GENERA OF GUTTIFERAE IN THE SOUTHEASTERN UNITED STATES

General characters: *plants with translucent or black secretory cavities present as dots or elongate sacs; sap resinous, yellowish, greenish, or clear; flowers perfect or imperfect, regular, hypogynous, 4- or 5-merous, usually in simple or compound dichasia; stamens numerous to few, distinct or united at base; gynoecium 2–10-carpellate; ovules anatropous; placentation axile, pseudoaxile, or parietal; fruit a septicidal capsule.*

A. Leaves thick, leathery, obovate, rounded or emarginate at apex, cuneate at at base; tree with viscid yellow sap; flowers imperfect; seeds arillate. . . . . 1. *Clusia.*

A. Leaves various, not as above; sap clear, not yellow; flowers perfect; seeds not arillate.

B. Petals yellow; staminodia lacking; stamen fascicles (when present) consisting of an unequal number of stamens; herbs, shrubs, or small trees. . . . . 2. *Hypericum.*

B. Petals flesh-colored, pinkish, or greenish; stamen fascicles 3, consisting of 3 stamens each, alternating with 3 staminodia; herbs. . . . . 3. *Triadenum.*

Subfam. CLUSIOIDEAE [Engler in Martius & Eichler, Fl. Brasil. **12**(1): 393. 1888.]

Tribe CLUSIEAE [Choisy in DC. Prodr. **1**: 557. 1824.]

1. **Clusia** Linnaeus, Sp. Pl. **1**: 509. 1753; Gen. Pl. ed. 5. 226. 1754.

Trees or shrubs, often epiphytic or half climbing on other trees and sometimes strangling them, with a viscid resinous yellow [or white] sap that flows from every part when cut. Leaves thick, leathery, rigid. [Inflorescences cymose or] flowers solitary and terminal. Flowers imperfect [? rarely perfect], the plants dioecious [or seldom polygamous]. Sepals 4[–6]. Petals [4–]6–9[–10], white or rose-colored. [Staminate flowers: stamens numerous, filaments united at base (or throughout), inner stamens often staminodial; gynoecium rudimentary or lacking.] Carpellate flowers: staminodia [5 to] many, united in a ring around the ovary [or free]; gynoecium of [5–]6–9[–10] carpels; styles short and thick or lacking; stigmas radiating; ovules numerous in each locule. Fruit thick, leathery or fleshy, subglobose in ours, capped by the persistent stigmas, at length capsular, dehiscent into as many valves as stigmas. Seeds inclosed in a fleshy aril; outer seed coat fleshy, inner seed coat leathery; cotyledons much reduced, the embryo consisting largely of radicle. LECTOTYPE SPECIES: *C. major* L. (*C. alba* Jacq.); see N. L. Britton, N. Am. Trees 700. 1908. (Name commemorating Charles de l'Écluse [Carolus Clusius], 1525–1609, author of *Rariorum plantarum historia*.) — BALSAM APPLE, PITCH APPLE.

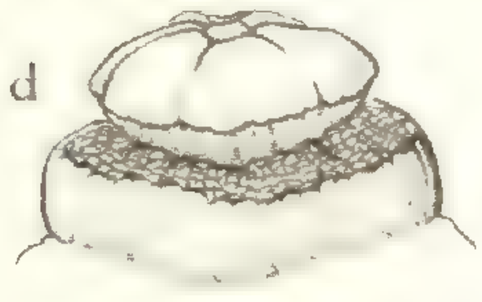
A genus of perhaps 100–200 species of the New World tropics and subtropics. In the most recent outline of the genus Engler (1925) recognized two subgenera and 17 sections. The taxonomy of the group is

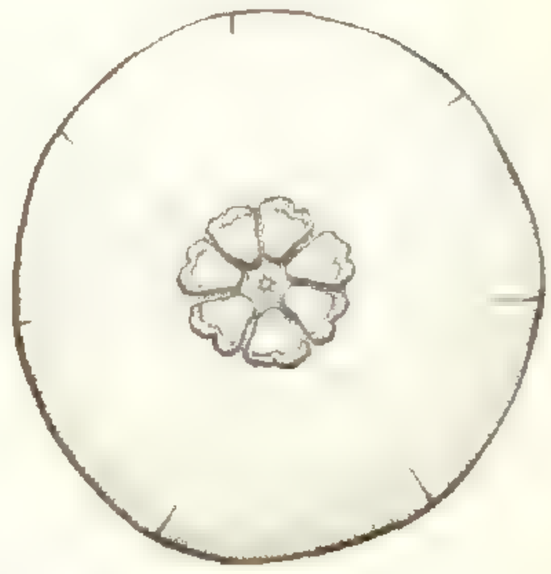
difficult, herbarium specimens are in many ways unsatisfactory for study, and dioecism poses additional problems.

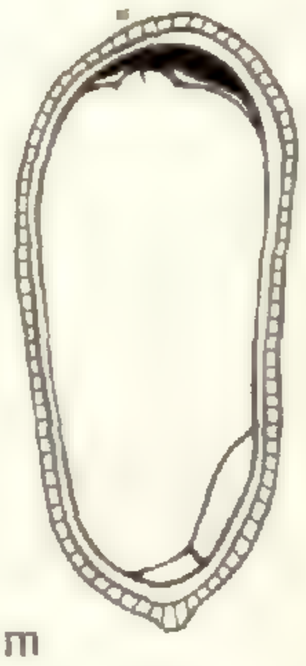
Clusia rosea Jacq., of subg. CLUSIA (subg. *Thysanoclusia* Vesque), sect. CHLAMYDOCLUSIA (Engler) Engler, is the only representative of the genus in the United States, where it is a rare plant on some of the Florida Keys. Reports of *C. flava* Jacq., of sect. CLUSIA (sect. *Stauroclusia* Planchon & Triana), from Key West are unsubstantiated, specimens so labeled being *C. rosea* instead (cf. Howard, 1962, p. 393). *Clusia flava* appears to be restricted to Grand Cayman and Jamaica. *Clusia rosea* is a Caribbean plant distributed from the Virgin Islands through the Greater Antilles to the Bahamas and southernmost Florida. In Florida it was first collected at Key West (where it was long ago exterminated), and it has since been found on Sugarloaf, Cudjoe, Little Torch, Big Pine, No Name, and Bahia Honda keys, Monroe County, *fide* George Avery, who notes that with the exception of the stations on Big Pine and No Name keys, all of these localities are immediately adjacent to former habitations. The plant is also known as an introduction on Key Biscayne, Dade County. *Clusia rosea* is nowhere frequent on the Keys, and in at least some of these localities all of the plants appear to have been removed or destroyed. With the ever-increasing alteration of the Florida Keys by man, it is problematical whether this species will survive there as a wild plant.

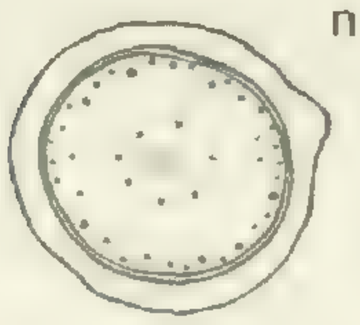
Under more favorable conditions than those in the Keys, *Clusia rosea* may become a tree up to 20 meters tall. It often begins as an epiphyte and grows like a strangling fig (*Ficus*). It is easily recognized by the very thick, leathery, obovate leaves that are either rounded or emarginate at the apex and cuneate at the base; by the copious yellow sap; and by the large, usually solitary flowers with six to nine white petals marked with pink. The plant is a handsome ornamental and is frequently cultivated in southern Florida, where only carpellate individuals seem to be present. Carpellate specimens set abundant fruit, however, and have viable seeds, embryos evidently being produced apomictically. Van Tieghem (1885) noted one to three embryos in seeds of *C. rosea*, and Vesque (1893, p. 110) found that seeds from a fruit that he examined were all polyembryonic. Seeds from a tree in the Fairchild Tropical Garden in Miami are also polyembryonic (see FIGURE 1, m, o, p). The distribution and frequency of staminate plants in the West Indies is very uncertain, but they appear to be rare or uncollected. None are represented in the collections of the Arnold Arboretum and the Gray Herbarium (but see Little & Wadsworth, 1964, under family references).

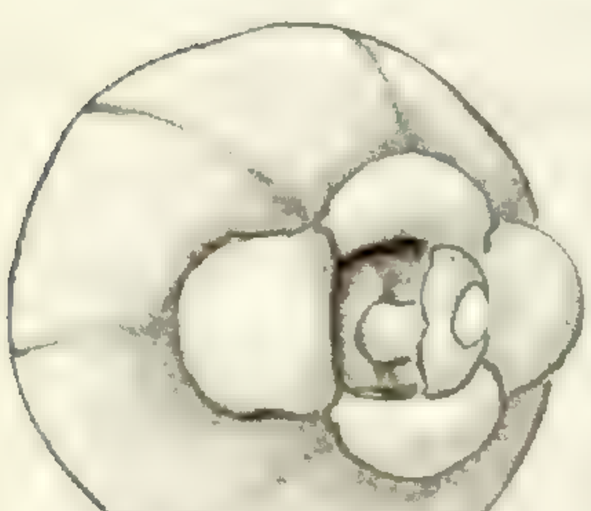
In carpellate flowers of *Clusia rosea* the numerous staminodia are almost completely fused together in a ring around the ovary. At anthesis they begin to deliquesce from the tips downward into a sticky, brownish, opaque mass that attracts bees. Both the conspicuous aril around the seed and the fleshy outer seed coat are bright orange, and the seeds are undoubtedly bird-dispersed. The embryo is notable for the greatly reduced cotyledons and relatively large radicle (cf. FIGURE 1, m).











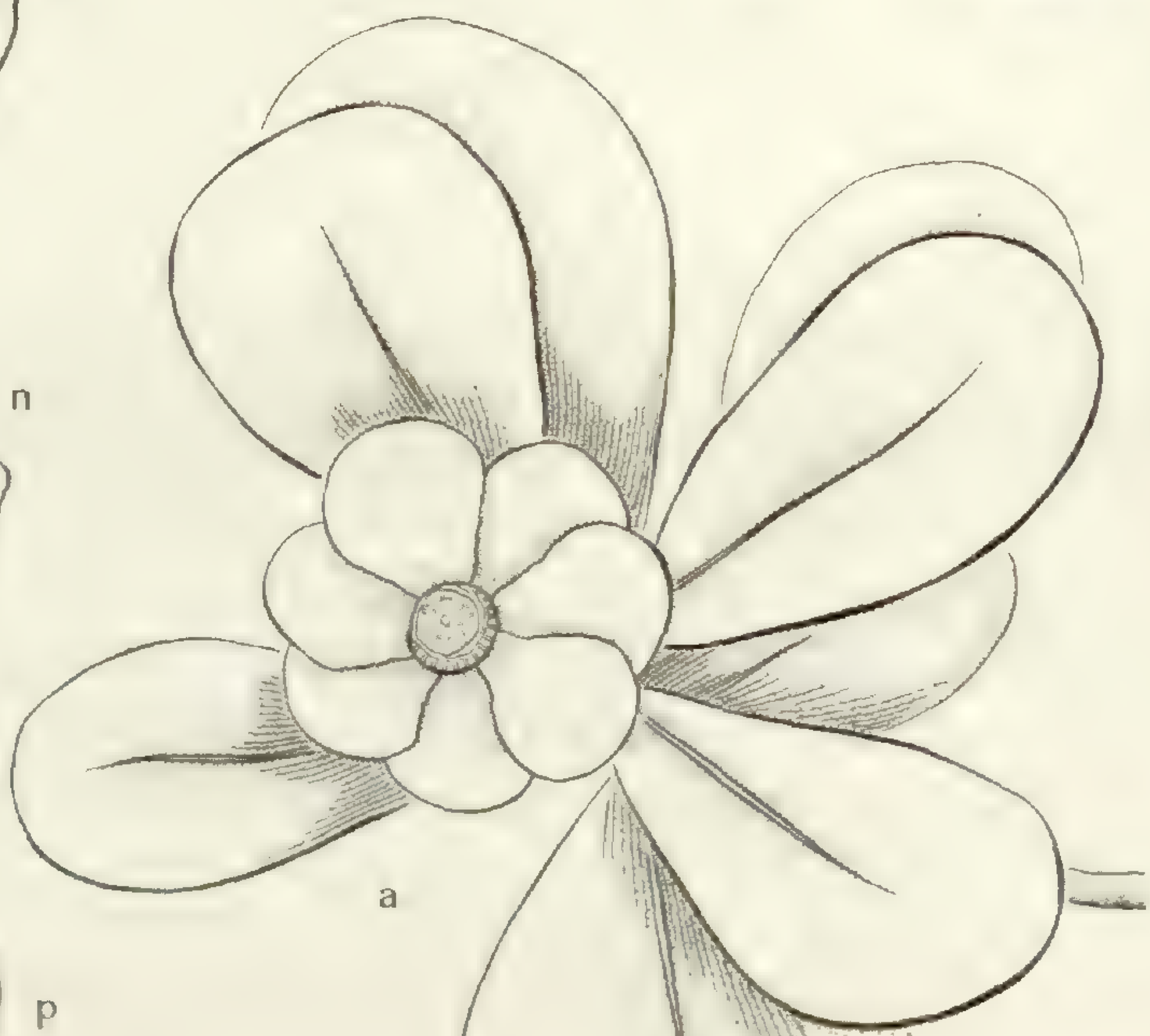


FIGURE 1. **Clusia.** a–p, *C. rosea*, carpellate plant only: a, branch with carpellate flower, × ¼; b, vertical section of carpellate flower bud — note overlapping petals, phalanges of staminodia to either side of ovary, numerous ovules in each locule of ovary, × 2; c, detail of "b" to show four rows of staminodia, × 3; d, gynoecium surrounded by staminodia — gummy, deliquesced upper

Collectors of *Clusia* species should note the color of the sap (yellow or white) that oozes from cut surfaces, for this characteristic is supposed to delimit major groups of species. Efforts should also be made to obtain specimens from both staminate and carpellate plants. No chromosome counts have been recorded for any member of the genus.

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part of staminodia removed (dissolved away with alcohol), × 1; e, cross section of ovary from older flower to show placentation — note numerous secretory ducts in ovary wall, × 2; f, branch with nearly mature fruit, × ¼; g, underside of unopened fruit with accrescent sepals (4) and pair of bracts at base of peduncle, × ½; h, fruit from above to show persistent accrescent stigmas, × ½; i, open capsule with arillate seeds, some near tips of woody valves, most stacked in locules, × ½; j, seed with aril, × 3; k, seed, outer seed coat fleshy, × 4; l, seed with outer coat removed, × 4; m, diagrammatic vertical section of polyembryonic seed, fleshy outer seed coat hatched, mature embryo with greatly enlarged radicle and small apical cotyledons filling most of seed, two much smaller embryos at lower right, × 6; n, cross section of seed through radicle of embryo — note numerous secretory ducts, × 6; o, smaller embryo from "m," radicle enlarging, × 12; p, smallest embryo from "m," × 12.

Subfam. HYPERICOIDEAE Engler in Martius & Eichler,
Fl. Brasil. **12**(1): 391. 1888.

Tribe HYPERICEAE Choisy, Prodr. Monogr. Fam. Hyperic. 37. 1821.

2. **Hypericum** L. Sp. Pl. 2: 783. 1753; Gen. Pl. ed. 5. 341. 1754.

Small trees, shrubs, subshrubs, perennial or annual herbs, generally lacking pubescence. Leaves sessile or clasping, elliptic, oblanceolate, narrowly linear or needlelike, with or without an articulation at base. Inflorescence usually a simple or compound dichasium; flowers perfect, sepals 4 or 5, rarely 3 or 6, persistent long after fruit maturity or deciduous at capsule dehiscence. Petals 4 or 5, rarely 3 or 6, yellow, convolute in the bud, deciduous soon after anthesis or long-persistent as withered remains. Stamens numerous, or only 5–10 (in small-flowered species), in 3 or 5 fascicles or the filaments united at their bases to form a shallow ring or narrow band, deciduous or persistent, staminodia present or absent. Gynoecium of 5 (4, 3) or 2 carpels; ovary ovoid, gradually contracted into a stout persistent style, unilocular or partially divided by intruding placentae, or completely 3–5-locular. Capsule globose, ovoid or conic. Seeds short-cylindric; seed coats finely to coarsely reticulate, occasionally obscurely striate. (Including *Ascyrum* L., *Crookea* Small, *Sarothra* L., and *Sanidophyllum* Small.) LECTOTYPE SPECIES: *H. perforatum* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 529. 1913. (*Hyperikon*, an ancient Greek name, probably for a species of this genus.) — ST. JOHN'S-WORT.

A genus of some 300 species of the subtropics, the highland areas of the tropics, and the warmer regions of the temperate zones. Represented in our area by about 40 species.

Hypericum, as delimited in this treatment, is broadly conceived to include *Ascyrum*, *Sarothra*, *Crookea*, and *Sanidophyllum*. Support for this concept of the genus comes from intensive studies by Robson and by Adams on the floral anatomy and taxonomy of *Hypericum*, various generic segregates, and related genera.

A satisfactory infrageneric taxonomy of *Hypericum* has been most difficult to achieve. Traditionally, flower structure has been used, especially the presence or absence of staminodia and the degree of fasciculation of the stamens. Using these and other characters, Keller (in Engler, 1925) recognized 18 sections within the genus (as delimited by him). Three of these, sect. HYPERICUM, sect. BRATHYS (Mutis ex. L. f.) Choisy, and sect. MYRIANDRA (Spach) Endl., are represented in our area. A fourth, sect. BRATHYDIUM (Spach) Endl., has been united with sect. MYRIANDRA by Adams.

Section HYPERICUM is represented in our area by the indigenous *H. punctatum* Lam., *H. Mitchellianum* Rydb., *H. graveolens* Buckley, and *H. pseudomaculatum* Bush and by the introduced and widely naturalized *H. perforatum* L. Members of this section have black dots and lines in

their leaves, sepals, and petals; stamens connate at the base into three or five fascicles; capitate stigmas; and three separate styles that are strongly divergent from the base.

Perhaps the best known of these species is *Hypericum perforatum*, $2n = 32$, a European plant that was first reported in the United States from near Lancaster, Pennsylvania, in 1793. In our area this plant is merely a somewhat bothersome weed in pastures and old fields and along roadsides, but in some of the Western States, especially in northern California, "Klamath weed" becomes a noxious pest on rangelands. The plants contain a photodynamic red pigment, hypericin, a napthodianthrone derivative, which if eaten by livestock sensitizes the white areas of the animal's skin to sunlight. Affected animals often develop body sores, swollen ears, and sore muzzles, and their weight and vigor are greatly reduced. Considerable progress has been made in the biological control of *H. perforatum*, especially by several species of beetles of the genus *Chrysolina* that have been introduced from Europe specifically for this purpose. These beetles feed on the plants, eventually killing them. The same control measures have been used successfully in Australia. Abundant seed production (an average of more than 23,000 seeds per plant) and prolific vegetative reproduction by both crown and root sprouts contribute to the aggressive weedy nature of *H. perforatum*. Apomixis has been discovered in European populations.

The 16 chromosomes of *Hypericum punctatum* and of *H. Mitchellianum* show ring formation of the *Oenothera* type at meiosis, a chromosomal behavior that is often a sign of structural hybridity. The closely related *H. graveolens* and *H. pseudomaculatum* are apparently normal cytologically.

Section BRATHYS is represented in our area by about 11 species of annual or perennial herbs belonging to subsect. SPACHIUM Keller. Members of this section are characterized by translucent glands in leaves, sepals, and petals; stamens generally fewer than 20 and arranged in three to five obscure groups; styles separate to the base and widely divergent at anthesis; and capitate stigmas. A striking member of this group is *Hypericum setosum* L., a plant of wet pinelands on the Coastal Plain from Louisiana to southeastern Virginia and the only hairy *Hypericum* in North America. Another interesting species of sect. BRATHYS, *H. cumulicola* (Small) P. Adams, the single species of *Sanidophyllum*, is a wiry herbaceous perennial known only from the *Pinus clausa* scrub of Highlands County, Florida. In its morphology and ecology, it seems to be most closely related to *H. gentianoides* (L.) BSP. (*Sarothra gentianoides* L.), which occurs over much of the eastern United States and disjunctly in Belize (*H. aphyllum* Lundell) and Brazil. It is clear that *H. cumulicola* represents merely an extreme evolutionary development within the section. Similarly, *H. gentianoides* and *H. Drummondii* (Grev. & Hooker) Torrey & Gray, closely related annuals of eastern North America assigned by Small to *Sarothra*, are clearly members of sect. BRATHYS allied to the *H. canadense–H. denticulatum* complex.

Two different chromosome levels are known in sect. BRATHYS in eastern North America. A diploid number of 16 occurs in *H. boreale* (Britton) Bicknell, *H. mutilum* L., *H. majus* (Gray) Britton, and *H. canadense* L., while $2n$ equals 24 in *H. gentianoides* and *H. denticulatum* Walter. Counts are needed for the other species of the section.

Intensive study of sect. BRATHYS is needed for a satisfactory delimitation of the species. Many of the taxonomic difficulties may be the result of extensive hybridization. According to Fernald, *H. mutilum* hybridizes with *H. gymnanthum* Engelmann & Gray, *H. majus*, and *H. canadense*, while *H. canadense*, in turn, crosses with *H. boreale* and *H. majus*. Fernald suggested that *H. dissimulatum* Bicknell is "perhaps an unusually constant and recurrent hybrid" of *H. canadense* with either *H. boreale* or *H. mutilum*.

Section MYRIANDRA is represented in our area by about 30 species of trees, shrubs, and herbaceous perennials. Plants of this section have styles that are closely appressed along their entire length at anthesis, minute stigmas (i.e., noncapitate ones), and translucent secretory cavities (dots or elongate sacs) throughout the plant body.

The taxonomy of sect. MYRIANDRA has been altered considerably by Adams, who has extended the limits of subsect. CENTROSPERMA Keller (in Engler, 1895) to include nearly all of the species of subsect. SUTUROSPERMA Keller. Thus enlarged, subsect. CENTROSPERMA includes 15 species of shrubs that have leaves and sepals with an articulation or groove at the base. Subsection SUTUROSPERMA has been altered to include the remnants of Keller's original subsection, plus the species formerly assigned to sect. BRATHYDIUM (Spach) Endl. and those placed in *Ascyrum* and *Crookea*: *H. stans* (Michx.) Adams & Robson (*Ascyrum stans* Michx.), *H. Edisonianum* (Small) Adams & Robson (*A. Edisonianum* Small), *H. tetrapetalum* Lam. (*A. tetrapetalum* (Lam.) Vail), *H. Hypericoides* (L.) Crantz (*A. Hypericoides* L.), *H. stragulum* Adams & Robson (*A. multicaule* Michx.), *H. suffruticosum* Adams & Robson (*A. pumilum* Michx.), *H. microsepalum* (Torrey & Gray) Gray ex S. Watson (*Crookea microsepalum* (Torrey & Gray) Small). As thus delimited, subsect. SUTUROSPERMA includes 15 species of shrubs and perennial herbs, the leaves and sepals of which lack an articulation or groove at the base. The redefined sect. MYRIANDRA appears to be a very natural group, within which *Ascyrum* and *Crookea* are only extreme evolutionary developments.

One group of closely related species in sect. MYRIANDRA, the *Hypericum fasciculatum* complex, has long been difficult taxonomically. Within the group Adams has distinguished eight species, each with a distinctive geographic range and specific habitat requirements. These eight (*H. fasciculatum* Lam., *H. lissophloeus* P. Adams, *H. Chapmanii* P. Adams, *H. nitidum* Lam., *H. brachyphyllum* (Spach) Steudel, *H. reductum* P. Adams, *H. Lloydii* (Svenson) P. Adams, and *H. exile* P. Adams) most likely share a common ancestry. They appear to be related through *H. galioides* Lam. to *H. densiflorum* Pursh and other members of subsect.

CENTROSPERMA. Additional studies, especially of the anatomy of the leaves, bark, and wood, are needed for a full understanding of infraspecific variation and a better delimitation of the species.

Three members of this complex native to western Florida (*H. Chapmanii* [Wakulla–Liberty counties west to Santa Rosa County], *H. nitidum* [western Florida; Baldwin County, Alabama; southern Georgia; Lexington County, South Carolina; and Brunswick County, North Carolina], and *H. lissophloeus* [Bay and Washington counties, Florida]) are unusual in that they become small trees often three or four meters in height. The single treelike stem of *H. Chapmanii* is often 10–15 cm. in diameter, especially near the base, but much of the width is a long-persistent, soft, spongy bark which often reaches a thickness of 3 or 4 cm.

In twenty-four of the thirty species of sect. MYRIANDRA the diploid chromosome number is 18; the remaining six species have not yet been studied cytologically. This chromosome number is also recorded for several species of *Hypericum* in other sections in other regions of the world.

The flowers of several species of sect. MYRIANDRA are known to be pollinated by bumblebees, honey bees, and various kinds of smaller bees, which obtain pollen from the large number of stamens.

Several species of sect. MYRIANDRA are planted as ornamentals. *Hypericum Buckleyi* M. A. Curtis is valued as a rock-garden or ground-cover plant, while *H. frondosum* Michx. is grown for its large, showy flowers. *Hypericum prolificum* L. and *H. Kalmianum* are used as ornamentals, both for their showy flowers and their smooth, lustrous brown bark, which adds interest to the winter aspect of the garden. Other species of this section, including *H. densiflorum*, *H. lobocarpum* Gattinger, and *H. nudiflorum* Michx., are sometimes planted but are not well recommended.

Some hybridization appears to occur between species of sect. MYRIANDRA. *Hypericum lobocarpum* and *H. prolificum* are believed to hybridize occasionally where the ranges of the two overlap in central Arkansas. A highly variable population in a pasture at Highlands, North Carolina, may have originated from hybridization between cultivated plants of *H. prolificum* and *H. frondosum*. Some spontaneous hybridization may occur when two or more of these woody species are brought into the garden. Two such putative hybrids, *H.* × *Dawsonianum* Rehder (*H. lobocarpum* × *H. prolificum*) and *H.* × *arnoldianum* Rehder (*H. densiflorum* × *H. lobocarpum*) were discovered at the Arnold Arboretum of Harvard University (see Adams, 1972).

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3. Triadenum Rafinesque, Fl. Tellur. 3: 78. 1837.

Perennial rhizomatous herbs. Leaves sessile or petiolate, oblong, oblong-lanceolate or elliptic, without an articulation at base, lacking black secretory glands, but dotted with clear glands which often turn dark upon drying. Inflorescence dichasial. Flowers perfect. Sepals 5, nearly equal, persistent, without an articulation at base. Petals 5, imbricate (or intermediate between imbricate and valvate) in the bud, flesh-colored, pinkish, greenish [or white], never yellow, symmetrical, deciduous soon after anthesis. Androecium of 3 fascicles of 3 stamens each, alternating with 3 hypogynous glandular staminodia, the stamens persistent. Gynoecium 3-carpellate; styles 3, separate to the base and divergent; stigmas capitate; placentation axile; ovules numerous. Seeds cylindrical; seed coat finely reticulate; raphe inconspicuous, not forming a keel or wing. TYPE SPECIES: *T. virginicum* (L.) Raf. — MARSH ST. JOHN'S-WORT.

A genus of four or more species in eastern North America, eastern Asia (*Triadenum japonicum* (Blume) Makino [*Hypericum crassifolium* (Blume) Nakai, not *H. japonicum* Thunb.] and perhaps one or two others), and India (*T. breviflorum* (Wallich ex Dyer) Y. Kimura). It is represented in our area by four taxa that are treated either as species (Gleason) or as varieties of two species (Fernald): *T. virginicum* (L.) Raf. (*Hypericum virginicum* L.), $2n = 38$; *T. Fraseri* (Spach) Gleason (*H. Fraseri* Spach, *H. virginicum* var. *Fraseri* (Spach) Fernald); *T. tubulosum* (Walter) Gleason (*H. tubulosum* Walter, *T. longifolium* Small); and *T. Walteri* (J. F. Gmelin) Gleason (*H. tubulosum* Walter var. *Walteri* (J. F. Gmelin) Lott).

The species of *Triadenum* have long been assigned by most botanists to *Hypericum* sect. ELODEA (Juss.) Choisy, but several authors, including Holm, Small, and Gleason, have regarded this taxon as a distinct genus and have revived the long-unused Rafinesque name for it. As delimited by these workers, species of *Triadenum* differ from *Hypericum* in the petals, which are imbricate, rather than convolute, and pink to greenish, instead of yellow, and in the nine stamens in three fascicles of three each, with three alternating staminodia. Studies by Robson of the

FIGURE 2. **Triadenum.** a–e, *T. virginicum*: a, upper part of plant with nearly mature fruit, × ½; b, flower — note stamens in three's with alternating staminodia, × 5; c, cross section of ovary to show placentation, × 15; d, capsule after dehiscence, × 3; e, seed, × 25. f, *T. Walteri* (*T. tubulosum* var. *Walteri*), fascicle of stamens — compare with "b," × 12.

vascularization of the flower strongly suggest that the group is indeed sufficiently distinct from *Hypericum* to warrant treatment as a separate genus. Robson concluded that the species of *Triadenum* are actually more closely related to *Cratoxylon* than to *Hypericum*. The floral anatomy of *Triadenum* closely resembles that of *Cratoxylon*, from which, in his opinion, it is an herbaceous derivative.

An intensive taxonomic study of *Triadenum* would aid greatly in understanding the delimitation of the species and the variation patterns within each species. Additional chromosome counts are needed. Studies of the reproductive biology would also be of value.

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THE GENUS GYMNOCLADUS AND ITS TROPICAL AFFINITY

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THE CAESALPINIOIDEAE is generally regarded as a predominantly tropical subfamily of the Leguminosae. On the basis of a preliminary survey of some 180 genera listed by Heywood (1971), I am able to show (unpublished data) that about 79 (44.38 per cent)[1] are endemic to tropical Africa as compared to 44 (24.72 per cent) in tropical America and 26 (14.62 per cent) in tropical Asia. The abundance of endemic genera in tropical Africa indicates that this area may be the center of diversity for the subfamily. This view is well supported by a series of studies carried out by Léonard (1950, 1951, 1957), Hutchinson and Dalziel (1958), and Brenan (1965, 1967). On the other hand, tropical America, especially the Amazon Basin, has been suggested by Ducke and Black (1955; see also Langenheim, Lee, & Martin, 1973) as a secondary center of diversity for the subfamily Caesalpinioideae. The phytogeographical significance of the Asiatic Caesalpinioideae, however, has long been overlooked. With the 26 endemic genera occurring in tropical Asia, and the apparent affinity of these Asiatic representatives to African ones (12 genera are found exclusively in tropical Asia and Africa, the so-called Old World Tropics, in contrast to only two genera of this subfamily represented in both Asia and America), a comprehensive study of the Asiatic genera is not only desirable, but also necessary for an understanding of the evolutionary history of the subfamily.

Among the Asiatic genera, the Chinese taxa are of particular interest, as there are about 17 genera and some 80 species of Caesalpinioideae, representing a wide spectrum of diversity in their distributional pattern. For example, the monotypic genera *Lysidice* and *Zenia* are known only in tropical and subtropical China. *Erythrophleum*, *Cynometra*, *Saraca*, *Sindora*, *Intsia*, *Mezoneuron*,[2] *Pterolobium*, *Peltophorum*, and *Parkinsonia* are represented in tropical China by one or two species with much restricted distribution, whereas *Cercis*, *Gleditsia*, *Gymnocladus*, *Caesalpinia*, and occasionally several annual *Cassia* species have a much wider distribution, extending into the warm temperate regions as well (TABLE 1).

Since very little has been written in western literature about the Chinese tropical area and its phytogeographical significance, a brief review of the Chinese tropics and a summary of some of the more recent considerations of floristic affinities of the Chinese tropical areas to other parts of the world are given here.

The tropical area of China is restricted to a narrow zone along the southern border. It starts in southeastern Yunnan and extends eastward

[1] Brenan (1965) in a study of 81 genera of Caesalpinioideae listed 54, i.e. 66.66 per cent, as endemic to tropical Africa.

[2] Vidal and Thol (1974) consider *Mezoneuron* to be a subgenus of *Caesalpinia*.

TABLE 1. **Chinese genera of the Caesalpinioideae.***

	NO. OF SPECIES IN CHINA	DISTRIBUTION	REMARKS
Dimorphandreae			
Erythrophleum	1	Chekiang, Fukien, Kwangtung, Taiwan	
Caesalpinieae			
Caesalpinia	ca. 18	Shensi, Kiangsu, Anhwei, Chekiang, Hupeh, Hunan, Kiangsi, Fukien, Taiwan, Kwangtung, Kwangsi, Kweichow, Szechwan, Yunnan	
Gleditsia	7	Widely distributed in N.E., E., Central, S., & S.W. China	
Gymnocladus	2	Kiangsu, Anhwei, Chekiang, Hupeh, Hunan, Kiangsi, Fukien, Kwangtung, Kwangsi, Szechwan, Yunnan	
Mezoneuron	1	Yunnan, Kwangtung (Hainan)	
Parkinsonia	1	Kwangtung (Hainan)	Introduced?
Peltophorum	1	Kwangtung (Hainan)	
Pterolobium	1–2	Hupeh, Szechwan, Yunnan, Hunan, Kwangtung, Kwangsi	
Cassieae			
Cassia	ca. 13	N.E. China, Shantung, Hopeh, Fukien, Kwangtung, Kwangsi, Yunnan, Taiwan	
Zenia	1	Hunan, Kwangtung, Kwangsi, Kweichow, Yunnan	Endemic
Detarieae			
(Cynometreae)			
Cynometra	1	Kwangtung (Hainan)	
Intsia	1	Taiwan	
Lysidice	1	Kwangtung, Kwangsi, Kweichow, Yunnan, Taiwan	Endemic
Saraca	1–2	Kwangtung, Kwangsi, Yunnan	
Sindora	1	Kwangtung (Hainan)	
Cercieae			
(Bauhinieae)			
Bauhinia	ca. 25	Kansu, Chekiang, Hupeh, Hunan, Kiangsi, Fukien, Kwangtung, Kwangsi, Kweichow, Szechwan, Yunnan, Taiwan	
Cercis	6	Anhwei, Hupeh, Szechwan, Kweichow, Kwangtung, Kwangsi, Yunnan, Kansu, Liaoning, Shensi	

* Genera are arranged alphabetically by tribes. Tribal designation is according to that of Heywood (1971). Tribes without representatives in China are excluded.

via Kwangsi to the coastal provinces of Kwangtung and Fukien, including the offshore islands of Taiwan and Hainan, as well as the South Sea Islands. The boundary and even the existence of the Chinese tropics were subjects of controversial argument that stirred up considerable interest in several Chinese journals in the 1950's and early 1960's (see Chin, 1956; Yen, 1961; Young, 1961; Lou, Feng, & Chiu, 1961). In a brief review, Tsang (1964) pointed out that the confusion was due mainly to the use of different terminologies. He further concluded that although there is only a small equatorial tropical zone in China, a considerable area which may be classified as tropical is present. According to his scheme, the Chinese tropics are composed of two parts, the equatorial tropical zone and the tropical zone. The former may be subdivided into the equatorial zone and the equatorial monsoon zone, whereas the latter may be subdivided into the tropical monsoon zone and a transitional zone. On a regional basis, six districts are recognized: (1) the tropical mountainous area of southern Yunnan, (2) the limestone mountains of Kwangsi, (3) Hainan, (4) the highland along Kwangtung and Fukien, (5) Taiwan, and (6) the South Sea Islands (FIGURE 1). In spite of the regional differences, which are subject to various local factors, the floristic elements in these areas indicate a close relationship to the India-Burma flora, with the exception of those in Taiwan and probably the South Sea Islands, which show an affinity to the flora of the Philippines.

Evidence derived from floristic composition also supports the existence of a tropical flora in China. Members of the Annonaceae, Moraceae, Connaraceae, Flacourtiaceae, and Passifloraceae are very abundant in southern Yunnan and in Hainan (see Wu, 1965; Wu & Wang, 1957–1958; Wu & Li, 1965; Fedorov, 1958). Woody epiphytes, characteristic of tropical rain forests, are also abundant in the areas cited (Fedorov, 1959). According to Fedorov (1959), the rarity of members of the Dipterocarpaceae (represented by three species of *Hopea* and one species of *Vatica*) is due to historico-floristic factors rather than to climatic influence.

In a systematic survey of the Chinese caesalpiniaceous plants, *Gymnocladus* is chosen here for a more detailed study because it is a small genus composed of only four species and because it is the only genus of the Caesalpinioideae confined to eastern North America and eastern Asia. Although *Gymnocladus* is generally regarded as a genus of temperate areas, the presence of *G. burmanicus* and *G. assamicus* in the mountains of the tropical zone may indicate a strong tropical affinity for the genus. *Gymnocladus* has a rich fossil record, which, when combined with other information (e.g., that concerning the Tertiary climate and the present distribution of the genus), will facilitate interpretation of migration routes of the genus in the past.

TAXONOMIC HISTORY

The genus *Gymnocladus* was established in 1785 by Lamarck, in reference to the "naked branches" of the trees in winter. Lamarck cited two

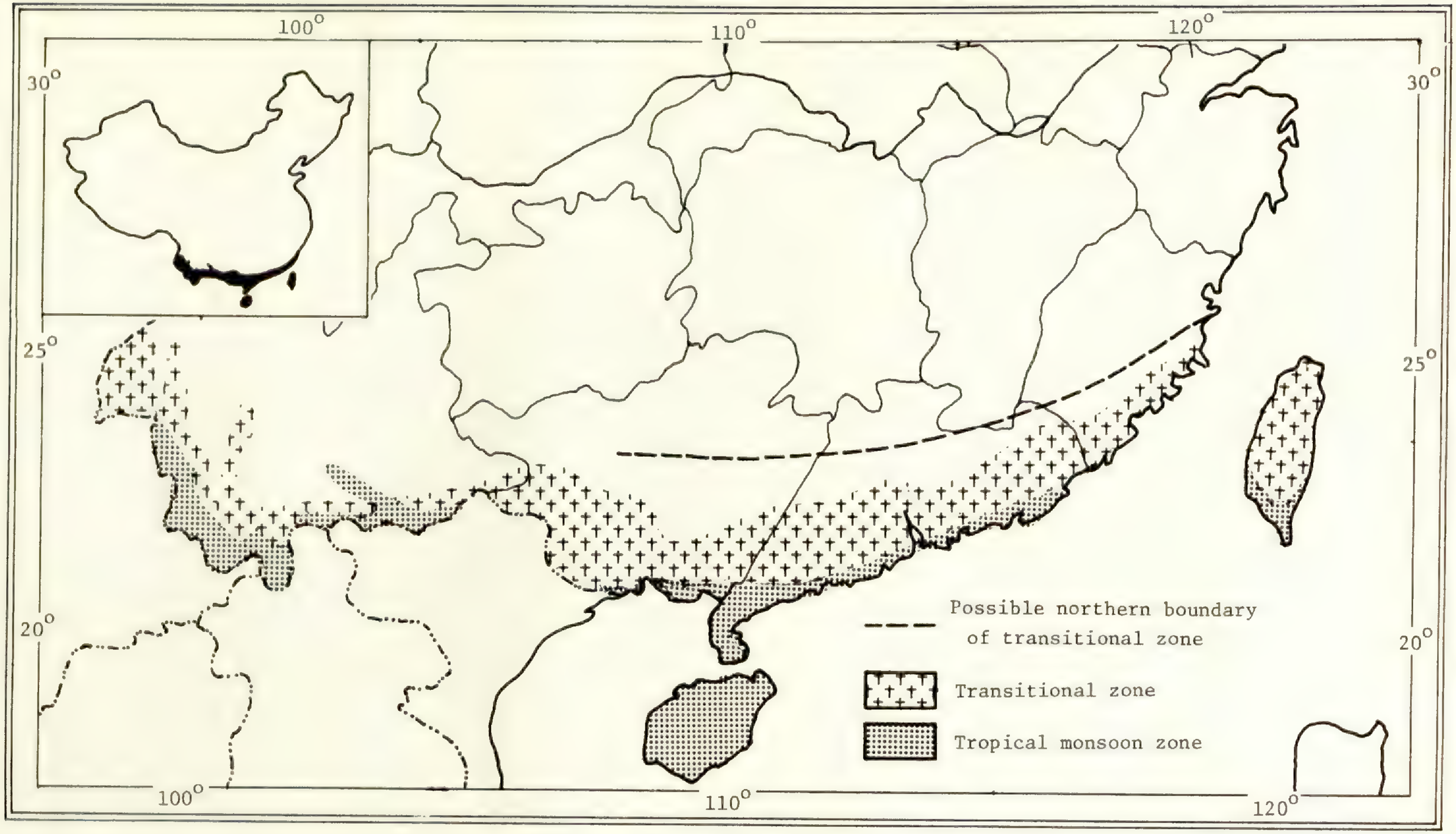

FIGURE 1. Tropical zones of China (according to Tsang, 1964, with minor modifications). Insert showing relative position of the Chinese tropical zones.

species under the genus, *G. canadensis* from eastern Canada and *G. arabicus* from Egypt. The plant which Lamarck called *G. canadensis* was known by some earlier botanists. It was mentioned by Linnaeus (1742, 1753) as *Guilandina dioica*. Duhamel (1755) described and illustrated the plant under the generic name "Bonduc" in his *Traité des Arbres*. Vahl (1790) referred both *Guilandina dioica* and *Gymnocladus canadensis* to his *Hyperanthera dioica*. It was not until 1869 that Koch transferred *Guilandina dioica* to *Gymnocladus* and recognized it as an earlier name for *Gymnocladus canadensis*. On the other hand, *Gymnocladus arabicus*, the second species of the genus described by Lamarck, is now considered to be synonymous with *Moringa aptera* of the Moringaceae. Baillon (1875) described *G. chinensis* from "Shanghai," China. *Gymnocladus Williamsii*, described from Peking, China (Hance, 1884), has been placed in synonymy with *Gleditsia sinensis* Lam. Two other species, *Gymnocladus burmanicus* and *G. assamicus*, have been described from Burma (Parkinson, 1928) and Assam, India (Kanjilal, 1934) respectively.

MORPHOLOGICAL CHARACTERS

HABIT. Deciduous trees from 6 to 20 meters tall. Bark silver-gray, occasionally tinged with red, deeply fissured or not; the pith of young branches purplish.

LEAVES. Leaves bipinnate, occasionally pinnate; stipules lanceolate or slightly obovate; petioles abruptly and conspicuously enlarged at the base, with 3–7 pairs of subopposite to opposite pinnae; leaflets in each pinna varying in number according to species, ovate, oblong to oblanceolate, entire, the apex acuminate to rounded, mucronate, the base cuneate to rounded, slightly oblique, the petiolules 2–4 mm. long, the midrib prominent only on the abaxial surface, with 6–8 pairs of secondary veins joined together in a series of arches (brochidodromous, FIGURE 3), the stipels small, awl-shaped, and persistent or absent.

INFLORESCENCE AND FLOWERS. Inflorescence racemose to occasionally paniculate, erect to pendulous, usually appearing with the new leaves, the branches and pedicels hoary-tomentose, usually longer in those with "perfect" flowers than in those with only staminate flowers. Staminate flowers characterized by a rather narrow floral tube, with 10 fertile stamens, rudimentary pistil usually present. In the morphologically bisexual flowers, the pistil is well-developed, whereas the majority of stamens are characterized by having poorly developed anthers with pollen absent or apparently abortive. Thus, most of the apparently bisexual flowers are, in fact, functionally unisexual. This phenomenon has been described as dioecism by abortion (see Sargent, 1892). Calyx tubular, with 10 longitudinal veins, the lobes 5–4, greenish, lanceolate, valvate, and not fully enclosing the petals within; petals 5–4, greenish to creamy white, occasionally purplish on the adaxial surface, imbricate in bud; stamens in

2 whorls, 5 long alternating with 5 short, inserted on the margin of the floral tube, the anthers uniform, orange or yellowish, all fertile or abortive, the filaments pilose near the base; pistil sessile to subsessile, covered with thin pilosity throughout, rudimentary or lacking in staminate flowers, the style short, erect, obliquely dilated or slightly capitate, ovules 4 to many. Pollen grains tricolporate, ellipsoid-oblong, the exine perforate-tectate, reticulate (FIGURE 2).

FRUIT. Oblong to falcate, turgid to compressed, woody to subwoody, smooth or ridged and grooved, dark brown, usually covered with a glaucous bloom, with endocarp pulpy (greenish and slimy when fresh), dehiscent along the placental suture when mature.

SEEDS. One to several, ovoid to subglobose, surrounded by the endocarpic pulp; funicle stout, ca. 5 mm. long; testa bony, dark brown; embryo straight, surrounded by a copious, cartilaginous endosperm, the cotyledons ovate, thick, and fleshy, the radicle short, erect.

SEEDLINGS. Germination of seeds hypogeous (at least in *G. dioicus*; see U.S.D.A., 1948); juvenile leaves once-pinnate.

GENERIC RELATIONSHIPS

The genus *Gymnocladus* was originally assigned to tribe Cassieae by De Candolle (1825a, b) under his suborder Caesalpinioideae of the family Leguminosae. It was later transferred to tribe Caesalpinieae (as Eucaesalpinieae) by Bentham (1840). Bentham's tribal classifications of the Caesalpinioideae have been accepted by many later workers. Hutchinson (1964), however, was dismayed by the seemingly minor and occasionally overlapping characters employed by Bentham in delimiting the tribes, and he reclassified the subfamily, relying heavily on the foliar characters. As a result, Hutchinson assigned most of the genera in the Caesalpinieae and Dimorphandreae (both *sensu* Bentham) to Group V of the Caesalpinioideae.[3]

In a recent summary Heywood (1971) listed 27 genera under tribe Caesalpinieae. My discussion here, however, will be limited to the relationship between *Gymnocladus* and *Gleditsia* for the following reasons. First, as indicated by Bentham (1866), both genera have polygamous flowers, with the calyx lobes not completely covering all the petals in the bud and some of the petals therefore almost having the appearance of sepals. This represents a very unusual (if not unique) condition in the Leguminosae. Secondly, *Gymnocladus* is usually placed close to *Gleditsia* in various taxonomic works (see De Candolle, 1825a, b; Bentham & Hooker, 1865; Taubert, 1891; Burkart, 1952), suggesting their close relationship.

[3] Hutchinson recognized five groups in the Caesalpinioideae, which together with his Brachystegioideae comprise the Caesalpiniaceae.

Gymnocladus and *Gleditsia* share many characters in common. Some of the striking similarities are the nature of the calyx, as mentioned by Bentham (1866), and the presence of the so-called polygamous flowers. Polygamy, when used without any clarification, is a rather confusing term. It has been defined as the condition of having staminate, carpellate, and hermaphrodite flowers on the same individual (Henderson & Henderson, 1963). The relative proportion of the three kinds of flower, however, may vary even among individuals within the same population. In the flowers of *Gymnocladus* and *Gleditsia*, usually only one type of reproductive organ is functional, although a rudimentary or abortive organ of the opposite sex may be present. This phenomenon may be interpreted as incomplete dioecism.

The morphological differences between the staminate and carpellate ("perfect") flowers and inflorescences in the various species of *Gymnocladus* are rather slight compared with the differences in the species of *Gleditsia*; the tendency toward dioecism is much greater in *Gleditsia* than in *Gymnocladus*. In *Gleditsia*, the staminate flowers are significantly different from the morphologically bisexual (but functionally carpellate) flowers. Although true polygamy has been reported for *G. triacanthos* in the literature (O'Rourke, 1949; Grisiuk, 1952), individual trees are characterized, for the most part, by their having only one kind of flower. *Gleditsia* should therefore be considered as a predominantly dioecious genus (Lee, unpublished manuscript). Further supporting evidence may be derived from the differentiation of two kinds of inflorescence which accompany the evolution of unisexual flowers in most species of the genus. The staminate inflorescence is spikelike, characterized by many small and highly congested flowers, whereas the carpellate ("perfect") inflorescence is a lax raceme with larger and many fewer flowers.

The seeds of *Gymnocladus* and *Gleditsia* are smooth, with hard testa and large amounts of cartilaginous endosperm surrounding the embryo. The endosperm consists of thick-walled cells, which upon the addition of water are converted into "mucilage" (see Pammel, 1899; Sayed & Beal, 1958). The presence of such endosperm suggests the close relationship of the two genera, although similar endosperm has also been found in some species of *Cercis*, *Hoffmannseggia* (Pammel, 1899), *Bauhinia*, and *Erythrophleum* (see Corner, 1951). The presence of copious endosperm is generally regarded to be a primitive character. This coincides with the seemingly undifferentiated flowers of *Gymnocladus* and *Gleditsia*, but it is in contrast to the occurrence of dioecism.

Gymnocladus and *Gleditsia* are known to lack nodule formation in their roots (see Allen & Allen, 1936), a character considered by Burkart (1952) to be "primitive." In a review of nodulation among leguminous plants, Allen and Allen (1961) indicated that only about 24 per cent of the 115 species (which represent 40 genera) form nodules. This percentage is significantly low when compared with percentages in the Mimosoideae and Faboideae (87 per cent in 146 species of 21 genera and 94 per cent in 1024 species of 182 genera respectively). In a recent study

of nodulation among Rhodesian leguminous plants, Corby (1974) revealed a similar low percentage of nodulation among members of the Caesalpinioideae. Thus, the lack of nodule formation should be regarded as significant at the subfamily level only. It may be the result of the tropical environment and the arboreal nature usually associated with the subfamily.

The two genera are also known for their richness in saponins. In fact, fruits of *Gymnocladus chinensis* and several species of *Gleditsia* are commonly used in China as soap substitutes. In this study an attempt has been made to use this character of the chemical constituents as an aid in classification. On the basis of a preliminary investigation of fruit saponins in the two genera, the aglycones (which together with various sugars are the products of hydrolysis of saponins) are found to be triterpenoid in nature (Parkhurst & Lee, unpublished data). Of the three species of *Gleditsia* (*G. triacanthos*, *G. sinensis*, and *G. officinalis*) and the three species of *Gymnocladus* (*G. dioicus*, *G. chinensis*, and *G. assamicus*) studied, a distinct set of aglycones was observed for each genus, although the quantity of each component varied in different species. Among the three *Gleditsia* species there are eight major components, with oleanolic acid as the predominant compound, whereas among the *Gymnocladus* species four major compounds are present. The triterpenoid aglycones found in *Gleditsia* are either lacking or significantly small in quantity in *Gymnocladus*, and *vice versa*. In other words, chemical characters (saponin chemistry) may be used to separate the two genera, but they have little value in delimiting various species of the same genus. This finding nevertheless indicates the homogeneity within each of the genera. The presence of structurally similar triterpenoid saponins in the two genera furthermore suggests a close affinity.

On the basis of the morphological characters (particularly the less differentiated flowers) and the nature of dehiscence of the fruit, it seems reasonable to conclude that in the tribe Caesalpinieae, *Gymnocladus* represents a more "primitive" genus than *Gleditsia*. This contrasts with the phylogenetic arrangement generally inferred (see Taubert, 1891; Burkart, 1952). However, this arrangement does not indicate that *Gleditsia* is derived from *Gymnocladus*.

Gymnocladus can be easily separated from *Gleditsia* by the nature of the fruit, which is dehiscent along the placental suture; by the erect, racemose inflorescence and the larger flowers; by the absence of spines on the trunk and branches; by the presence of small, awl-shaped, persistent stipels (Asiatic species only); and by the presence of triterpenoid aglycones with higher molecular weight. Other similarities and differences are listed in TABLE 2.

DISCUSSION

Of the four *Gymnocladus* species, *G. chinensis* and *G. dioicus* have disjunct distributions in the vast temperate areas of eastern China and the

eastern United States respectively. For this reason *Gymnocladus* has long been regarded as a genus of temperate regions. The two more recently described species, *G. burmanicus* and *G. assamicus*, have been overlooked in the literature. It is of particular interest that both of these species have a very restricted distribution, being found exclusively in the mountainous areas of the tropical zone of Asia. The species thus serve as

TABLE 2. **Comparison of Gymnocladus and Gleditsia.**

	Gymnocladus	Gleditsia
HABIT	Trees	Trees to shrubs
SPINES	Absent	Simple or compound
LEAVES	Bipinnate, rarely pinnate	Pinnate to bipinnate
EPIDERMIS	Margins sinuous	Margins straight
VENATION OF LEAFLETS	Brochidodromous	Craspedodromous to brochidodromous
FLOWERS	Predominantly dioecious	Predominantly dioecious
FLORAL TUBE	Tubular, elongated, hoary-pubescent	Short, turbinate, glabrate or pubescent
POLLEN	Tricolporate, exine reticulate	Tricolporate, exine reticulate
FRUIT	Oblong to falcate, dehiscent along placental suture	Oval to elongate, indehiscent to tardily dehiscent
PULP	Present	Present or not
TRITERPENOID SAPONINS	Present	Present
SEEDS	Large (ca. 1.5 × 1.5 × 1 cm.), subglobose	Small (ca. 1–1.5 × 0.5–0.8 × 0.3–0.5 cm.), subquadrate to obovoid
ENDOSPERM	Copious and cartilaginous	Copious and cartilaginous
GERMINATION	Hypogeal, juvenile leaves pinnate	Epigeal, juvenile leaves pinnate
CHROMOSOME NUMBER	$2n = 28$	$2n = 28$
NUMBER OF SPECIES	ca. 15	4
EXTANT GEOGRAPHICAL DISTRIBUTION	E. North America, E. & S.E. Asia, Burma and N.E. India	E. North America, Central South America, E. Asia extending to Malaya
REPORTED FOSSIL RECORDS	E. & W. North America, E. Asia, and Europe	E. & W. North America, E. Asia, and Europe

good indications of a tropical origin of the genus. A possible tropical origin of *Gymnocladus* is also supported by the overall tropical affinity of members of the subfamily Caesalpinioideae. Further evidence supporting such an origin of *Gymnocladus* may be derived from the floral structure of the genus. The predominantly dioecious flowers [4] of *Gymnocladus*, as exemplified by those of *G. dioicus*, are relatively large (flowering buds immediately before anthesis measured up to 1.8 cm. in length from the apices of the calyx lobes to the base of the floral tube, and 0.4–0.6 cm. in diameter at the widest part); are borne on a rather long and showy raceme or panicle; have a strong scent; bear abundant nectar within the floral tube; are frequently visited by small insects; and are characterized by the presence of an abortive/rudimentary organ of the opposite sex in both the staminate and carpellate flowers. All of these characteristics agree with the "syndromes" of the dioecious tree taxa in the tropics described by Bawa and Opler (1975) and contrast sharply with the usually very small, highly reduced, and predominantly wind-pollinated dioecious plants typical of temperate regions (e.g., the Amentiferae).

Furthermore, contemporary thinking in paleobotany indicates that plants regarded as "temperate" had broader and less definite ecological requirements, with their total geographical ranges larger than generally recognized, and they may have been associated with rather different ecotypes during various segments of their geographical history (Graham, 1972). This viewpoint again supports a possible tropical origin of the genus *Gymnocladus*. A similar situation may exist in a number of "temperate" genera, such as *Fagus*, *Liriodendron*, *Tilia*, *Nyssa*, and *Myrica*, which are also found in tropical or subtropical communities today.

The bicentric distribution of *Gymnocladus*, on the other hand, is part of the more elaborate distributional pattern known as the Tertiary relict disjunction, since fossil remains attributed to this genus have also been found in Europe and western North America. The long known eastern Asiatic–eastern North American floristic relationships have been discussed extensively in the past (see Gray, 1840, 1846; Fernald, 1929; Li, 1952; Graham, 1972; Wood, 1972) and will not be considered further here. However, with the discovery of two highly restricted species of *Gymnocladus*, *G. burmanicus* and *G. assamicus*, the "boundary" of eastern Asia becomes extended westward to include Assam and southern Yunnan, and southward to include Lower Burma. The presence of these two species of *Gymnocladus* in the mountainous regions of the tropical zone is of great phytogeographical significance, as they may be the remnant species of a once more widespread tropical stock.

In discussing ecological evolution of flowering plants and the origin of the temperate flora, Takhtajan (1969) suggested that angiosperms

[4] Dioecism is a rarity in the Caesalpinioideae. Other than in *Gymnocladus*, it has been found only in *Gleditsia* (Lee, unpublished data) and subg. *Guilandina* of *Caesalpinia* (Gillis & Proctor, 1974). All three of these genera belong to the tribe Caesalpinieae.

originated in monsoon countries with warm subtropical climates, i.e., in southern Yunnan and the adjacent areas of Tonkin and Assam. Although more information is needed to substantiate Takhtajan's hypothesis, recent works on the affinities of the Chinese tropical zone (Wu, 1965) and extensive floristic studies in southern Yunnan (Wu & Wang, 1957–1958; Wu & Li, 1965) indicate a high concentration of ancient tropical floristic elements in these areas.

On the basis of an extensive study of the tropical and subtropical flora of southern and southeastern Yunnan, Wu and Wang (1957–1958) proposed three possible migrational routes of the ancient (Tertiary) tropical flora of the southeastern Yunnan-Tonkin region. These are route 1: via Vietnam, Borneo, and the Philippines to Taiwan; route 2: via Kwangsi and Kwangtung to Hainan; and route 3: via Kweichow, Hopeh, and Szechwan to Kiangsu and Chekiang, and extending westward to the border of the Szechwan-Shikong highlands, with the northwestern boundary in Tsin-ling and Huai-ho. These routes, particularly "route 3," may be responsible for the "tropical floristic elements" presently found in the temperate regions of China.

Morphologically, particularly in foliar characteristics, the Asiatic species of *Gymnocladus* form a coherent group, which differs from its counterpart in eastern North America. Thus it is reasonable to assume that the separation of the two groups took place quite early. In addition, the presence of two upland species in eastern Asia may be explained by the gradual, rather recent orogenesis and the relatively stable climate in the southwestern border area of China. These conditions seem to provide a more favorable environment for conserving a greater number of species than those in eastern North America.

With the exception of its being dioecious, the genus *Gymnocladus* possesses several presumably primitive characteristics: its flowers are relatively undifferentiated, with five or four subequal calyx lobes and the same number of petals; its fruits dehisce along the adaxial (placental) suture, resembling a follicle; its seeds have copious endosperm; and its leaves have a subopposite to opposite arrangement of leaflets. All of these characteristics suggest that the genus represents a relatively primitive group within the Caesalpinioideae. Hence the association of dioecism with such a group may serve as indirect evidence for the early occurrence of this derived character.

TAXONOMIC TREATMENT

Gymnocladus Lamarck, Encycl. Méth. Bot. 1: 733 (in part). 1785; Tableau Encycl. Méth. II. 5(1): *pl. 823*. 1793; *Ibid*. III. 412. 1796.

Guilandina L. Sp. Pl. 381 (in part). 1753.
Hyperanthera Vahl, Symb. Bot. 1: 30 (in part). 1790.

Unarmed trees. Leaves deciduous, bipinnate, the stipules lanceolate to obovate, or absent; leaflets obovate, oblong to narrowly oblanceolate,

the two stipels small, awl-shaped and persistent, or absent. Inflorescence racemose to paniculate, terminal or axillary. Flowers regular, predominantly dioecious to polygamous, pedicellate, the bracts and bracteoles minute, pointed, deciduous or not; calyx tubular, ridged, 5-lobed; petals 5 or 4, creamy white or purplish; stamens 10, inserted on the calyx tube, with fertile anthers or not; ovary sessile, 4- to many-ovuled, rudimentary or absent in the staminate flowers. Fruit oblong to falcate, turgid to compressed, woody, pulpy inside, 1- to several-seeded, dehiscent along the placental suture. Seeds ovoid to subglobose, with stout funicles and thick, bony, dark brown testa; endosperm present.

TYPE SPECIES: *Gymnocladus canadensis* Lam. = *G. dioicus* (L.) K. Koch.

The original description of the genus includes both *Gymnocladus canadensis* and *G. arabica*, but later exclusion of *G. arabica* leaves *G. canadensis* (*G. dioicus*) as the type of the genus.

KEY TO THE SPECIES OF GYMNOCLADUS

1. Mature leaflets ovate, acuminate; widest part of leaflets exceeding 2 cm.; stipels absent (North American species). ..... *G. dioicus.*
1. Mature leaflets oblong to oblanceolate, rarely lanceolate, obtuse to slightly retuse, occasionally acute; widest part of leaflets never exceeding 2 cm.; stipels small, awl-shaped, and persistent (Asiatic species).
   2. Leaflets oblanceolate to lanceolate, acute to pointed; pinnae usually in 3 pairs. ..... *G. burmanicus.*
   2. Leaflets oblong, obtuse to slightly retuse; pinnae in 3–7 pairs.
      3. Fruit falcate, the pericarp with apparent ridges and grooves showing seeds within. ..... *G. assamicus.*
      3. Fruit oblong to subfalcate, the pericarp more or less smooth. ..... *G. chinensis.*

Gymnocladus dioicus (L.) K. Koch, Dendrology 1: 5. 1869.

FIGURE 2.

Guilandina dioica L. Sp. Pl. 381. 1753.
Gymnocladus canadensis Lam. Encycl. Méth. Bot. 1: 733. 1785; Tableau Encycl. Méth. II. 5(1): *pl. 823.* 1793; *Ibid.* III. 412. 1796.
Hyperanthera dioicus (L.) Vahl, Symb. Bot. 1: 31. 1790.

Trees 10–30 m. tall, the bark deeply fissured, dark gray throughout or tinged with red, 2 to 3 cm. thick. The rachis of the leaves 60–90 cm. long, glabrate or tomentose, with 5 to 7 pairs of pinnae 15–25 cm. long; pinnae 4–7-jugate, the lower pairs with single leaflets; leaflets ovate, 5–6.5 × 2.5 cm., or those replacing the lowest or occasionally the 2 lower pairs of pinnae sometimes twice as large, glabrate on both surfaces, with the exception of a few scattered hairs along the midrib, the apex short-acuminate, the base cuneate or rounded, slightly oblique, stipels absent. Inflorescence of the staminate flower 7.5–10 cm. long; inflores-

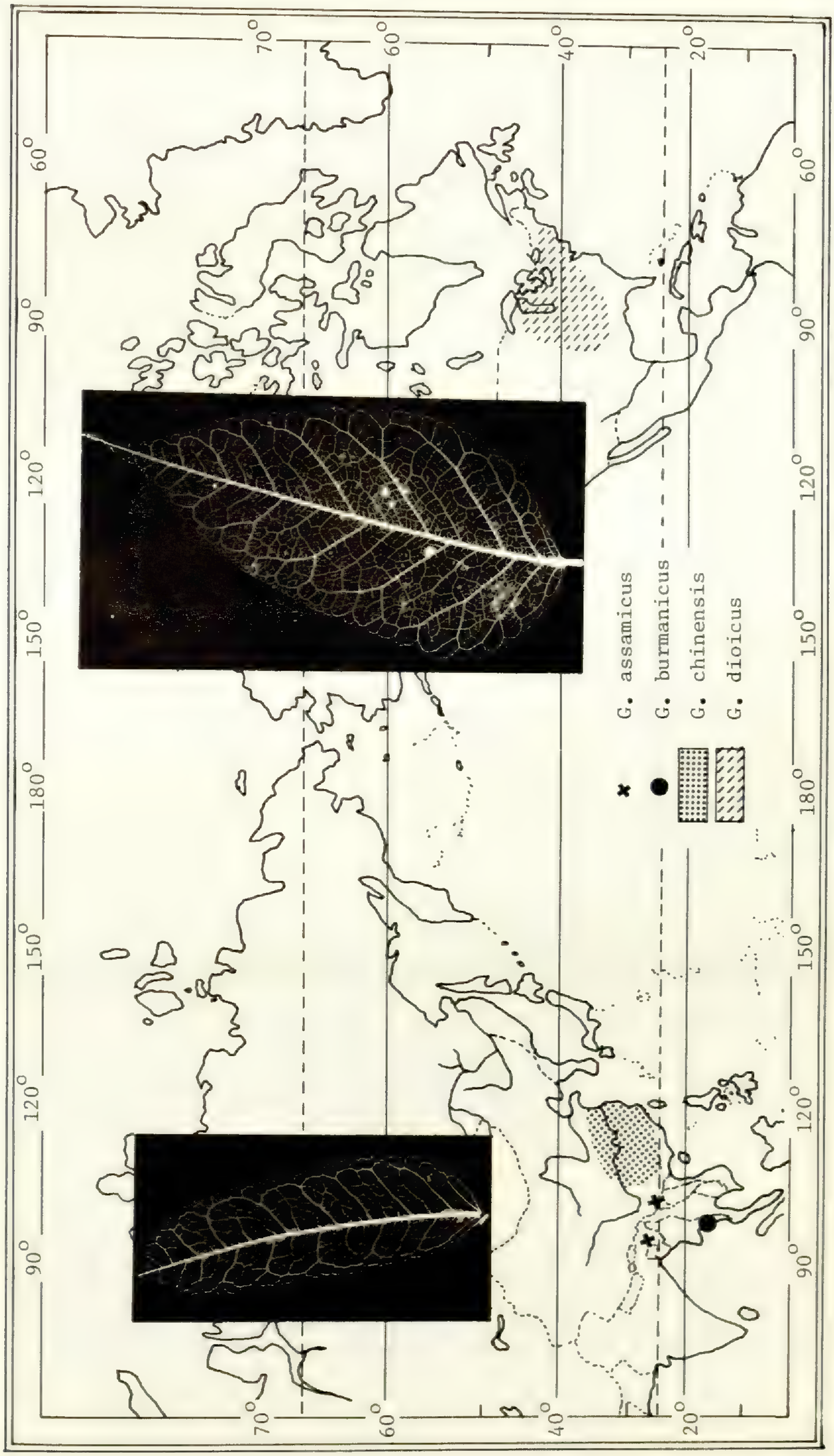

FIGURE 2. Distribution of the genus *Gymnocladus*. Inserts showing venations of *G. chinensis* (left) and *G. dioicus* (right).

cence of the carpellate ("perfect") flower 25–30 cm. long, the branches hoary-tomentose. Flowers on stout pedicels 1.5–2 cm. long or longer in the staminate flowers, with strong fragrance; calyx tube 6–12 mm. long, the lobes 5–4, lanceolate, 4–6 mm. long; petals 5–4, 5–7 mm. long, 1.5–2.5 mm. wide, slightly keeled, pilose on the back, tomentose on the inner surface, greenish white; stamens ca. 5 mm. long, the anthers orange to yellowish, fertile or abortive; ovary with scattered whitish pilosity, elongate, with 2–8 ovules, rudimentary or absent in the staminate flowers, the stigma slightly bilobed, acuminate at the apex. Fruit oblong to slightly falcate, 15–25 cm. long, 3.5–5 cm. wide, and 1–2 cm. thick, dark brown, covered with a glaucous bloom, on a stout stalk 2.5–5 cm. long, pulpy inside (the pulp greenish when fresh, turning yellow to brownish in age). Seeds 1–6, ca. 1.5–2 cm. long, 1.5–2 cm. wide, and 0.6–0.8 cm. thick. Chromosome number $2n = 28$.

TYPE. In the protologue of *Guilandina dioica* (Linnaeus, 1753), the only reference to earlier literature is that to the second edition of the *Genera Plantarum* (Linnaeus, 1742). In this earlier reference Linnaeus mentioned that he had seen male plants of this species growing in Paris and that fruits were common in museums. There is no material referable to *Guilandina dioica* in Linnaeus's herbarium, but it is possible that fruiting material which he saw is still extant. Hence *Gymnocladus dioicus* may be typified, at least for the time being, by Linnaeus's description in the second edition of *Genera Plantarum* (1742, p. 518).

The name *Gymnocladus canadensis*, on the other hand, is superfluous, since Lamarck referred to *Guilandina dioica* L.

HABITAT AND DISTRIBUTION. This bottomland species is found from central New York and Pennsylvania west through southern Ontario and southern Michigan to the valley of the Minnesota River, eastern Nebraska, Kansas, and western Oklahoma, and south between the Mississippi River and the Allegheny Mountains to Tennessee (Pinchot, 1907).

VERNACULAR NAMES. Kentucky coffee-tree (U.S.) and chicot (Canada).

REPRESENTATIVE SPECIMENS. **U.S.A.** ALABAMA: northeast of Sheffield, Colbert Co., Oct. 7, 1934, *Harper 3273* (GH). ARKANSAS: Cotter, Marion Co., Sept. 1, 1915, *Palmer 8406* (A); Shirley, Van Buren Co., May 28, 1924, *Palmer 25204* (A). ILLINOIS: near Shawneetown, Gallatin Co., June 6, 1919, *Palmer 15522* (A); Alto Pass, Union Co., May 3, 1919, *Palmer 15037* (A). IOWA: near Burlington, Des Moines Co., Sept. 5, 1921, *Palmer 20331* (A); Sidney, July 12, 1925, *Pammel 414* (GH). KANSAS: near Neodesha, Wilson Co., May 5, 1922, *Palmer 21140* (A); Riley Co., Oct. 2, 1895, *Norton 124a* (GH). KENTUCKY: Mt. Sterling, Montgomery Co., May 24, 1926, *Horsey 2313* (A); Richmond, Madison Co., May 15, 1920, *Horsey 1064* (A). MARYLAND: Baltimore Co., Sept. 1980, *Taylor s.n.* (GH). MICHIGAN: Hubbordston, Ionia Co., Sept. 6, 1890, *Wheeler s.n.* (A). MISSOURI: near Forest City, Holt Co., June 12, 1924, *Palmer 25401* (A); Red Oak, Lawrence Co., May 1, 1925, *Palmer 26977* (A). NEW YORK: Syracuse, Oct. 6, 1935, *Brown 8009A* (A); Tompkins Co., July 19, 1915, *MacDaniels 4395* (GH). NORTH CAROLINA: Mecklenburg Co., May

13, 1968, *Matthews et al. s.n.* (GH). OHIO: near Cincinnati, May 27, 1890, *Lloyd s.n.* (GH); Buena Vista, Sept. 14, 1936, *M. C. Smith 8242* (A). OKLAHOMA: Canton, Aug. 16, 1915, *Andrews 56* (A); near Tonkawa, Kay Co., Aug. 4, 1913, *Stevens 1829* (A). TENNESSEE: near Nashville, May, 1880, *Gattinger s.n.* (A); near Pegram, Cheatham Co., April 24, 1929, *Palmer 35508* (A). VIRGINIA: northwest of Return, Oct. 15, 1941, *Fernald & Long 13956* (GH). WEST VIRGINIA: Dickson, Wayne Co., July 20, 1936, *Gilbert 494* (GH). WISCONSIN: west of Milwaukee, Oct. 3, 1918, *Slavin 476* (A); south of Oshkosh, Winnebago Co., July 19, 1934, *Fassett & Truman 16869* (GH). **Canada.** ONTARIO: Norfolk Co., June 25, 1941, *Soper 2636* (GH); Lambton Co., Aug. 11, 1941, *Soper 2831* (GH); Pelee Island, July 28, 1892, *Macoun s.n.* (GH).

Although distributed over a wide area, *Gymnocladus dioicus* is one of the rarest of the forest trees of eastern North America (Sargent, 1892). It occurs usually as a single tree or in small clusters in localities most favorable to its growth. Over large areas within its range it is entirely lacking or represented only by an occasional individual (Pinchot, 1907). The range of this species is suspected by some to be associated with Indian camp sites or with the lands of the early settlers (Robert Bye, pers. comm.). Pinchot, however, indicates that the economic planting range of this species coincides with the natural range and may in places be extended beyond it.

The tree is often cultivated for ornamental purposes. The fruits, preserved like those of the tamarind, are said to be wholesome and slightly aperient (Hedrick, 1919). It should be cautioned that although the pod and particularly the pulpy tissue, which are rich in saponins, may be harmless when taken internally, painful death would result if an aqueous extraction of the fruit were injected intravenously, since the saponin in the solution lysolizes the red blood cells even in an extremely low concentration. Roasted seeds of *Gymnocladus dioicus* were employed by the early settlers of Kentucky as a substitute for coffee (Browne, 1846).

Gymnocladus chinensis Baillon, Compt. Rend. Assoc. Franç. Avanc. Sci. 3: 418–427. *t. 4.* 1875. FIGURE 2.

Trees 5–12 m. tall, the bark gray, usually smooth. The rachis of the leaves 25–30 cm. long, shortly and sparsely pubescent to glabrate, with 3–5 pairs of pinnae 14–28 cm. long; pinnae 10- to 12-jugate; leaflets oblong to elongate-oblong, 1.5–4 × 1–1.5 cm., densely whitish-tomentose on both sides when young, becoming glabrate with age, the apex rounded or slightly retuse, the stipels 1, ca. 1 mm. long, awl-shaped, and persistent. Inflorescence 4–10 cm. long, hoary-tomentose. Flowers with pedicel 1–2 cm. long, erect or pendulous; calyx tube 5–6 mm. long, the lobes lanceolate, ca. 4 mm. long, 2 mm. wide; petals oblong, ca. 5 mm. long, 2 mm. wide, lilac-purple; stamens ca. 4 mm. long, pilose near the base; ovary elongate, glabrate, usually 4-ovulate, rudimentary or absent in the staminate flowers, the style short, the stigma recurved-capitate. Fruit oblong, 7–12 cm. long, 3–4 cm. wide, and ca. 1.5 cm. thick, shortly

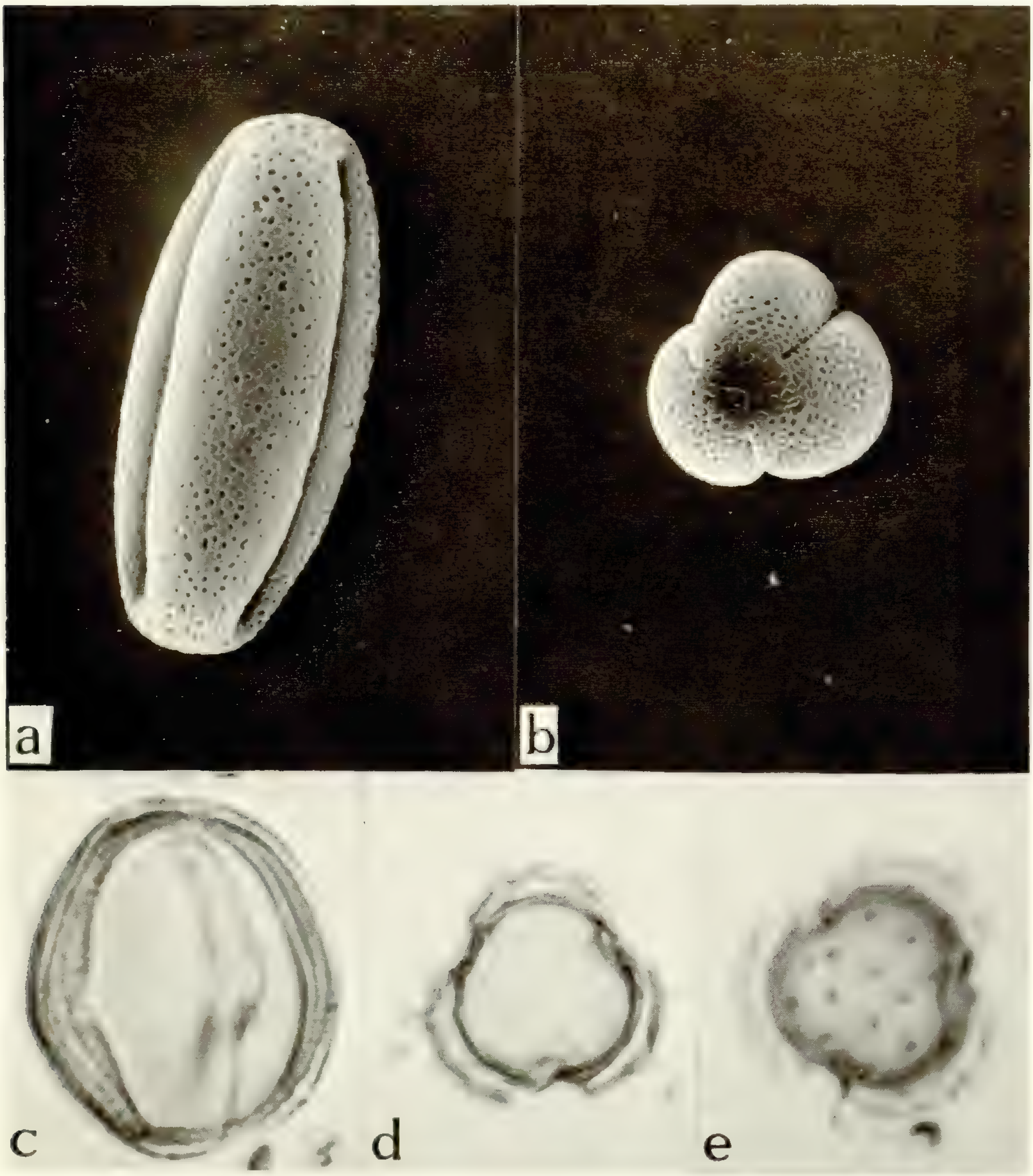

FIGURE 3. Pollen grains of *Gymnocladus dioicus*: a & b, SEM micrographs, pollen untreated, ca. × 1400; c–e, light microscope micrographs, pollen acetolized, ca. × 1000.

beaked, dark brown, usually covered with a glaucous bloom. Seeds 2–4, subglobose to ovoid, 1.5–2 cm. long, 1.5–1.8 cm. wide, and 1–1.2 cm. thick.

TYPE. Since no specimen of *Gymnocladus chinensis* is known in existence in the Baillon Herbarium, Laboratoire de Phanérogamie, Paris, the figure that appeared in the original article (Compt. Rend. Assoc. Franç. Avanc. Sci. 3: 418–427. *t. 4.* 1875) is designated here as the type of the species.

HABITAT AND DISTRIBUTION. *Gymnocladus chinensis* is the most widely distributed species of the genus. It has been reported in central and southeastern China, in the provinces of Anhwei, Chekiang, Fukien, Hunan, Hupeh, Kiangsi, Kwangtung, and Szechwan.

VERNACULAR NAMES. Fe-tsaou-tow and yu-tsao-chio (China).

REPRESENTATIVE SPECIMENS. **China.** ANHWEI: Chiu Hwa Shan, Aug. 21, 1934, *Fan & Li 284* (A, E); Huang Shan, Jan. 11, 1964, *H. Chiu 163* (PE). CHEKIANG: Howchow, Oct. 12, 1928, *Chiao 18894* (A, US); region 20 to 40 miles west of Wenchow, June 6–8, 1924, *Ching 1891* (A); between Ping Yung and Tai Suan, July 20, 1924, *Ching 2174* (A). FUKIEN: Yenping, June 20, 1925, *Ching 3480* (A). HUNAN: Yi Chang Hsien, May 1–13, 1934, *Tsang 23793* (US). HUPEH: Oct. 1887, *Henry 2873* (A, K), *Henry 5576a* (A); Nan-T'o and mountains to northward, *Henry 3873* (A, K); western Hupeh, Patung, May 1907, *Wilson 760* (A); Hsing-Shan Hsien, May 6, 1907, *Wilson 760* (A), Dec. 1907, *Wilson 760* (A), and other specimens labeled *Wilson 760* with various localities and dates in A, E, K, NY, and US. KIANGSI: Kiukiang, Aug. 1909, *Wilson 1598* (A, E). KWANGTUNG: Tsung-fa Hsien, Sam Kok Shan, May 1–25, 1935, *Tsang 25144*. SZECHWAN: 1885–1888, *Henry 5576* (E, US); Omei Hsien, Mt. Omei, 1891, *Feber s.n.* (LE); Aug. 25, 1928, *Fang 3342* (A, P, PE).

The fruit of *Gymnocladus chinensis* is highly esteemed for its saponaceous qualities and is much desired as a soap substitute in China. It is also used as an herb medicine in curing swellings and abscesses. Oil from seeds is used as latex in making paints.

Gymnocladus chinensis and the rest of the Asiatic species form a coherent group within the genus, and they may be easily separated from the American species, *G. dioicus*, by their much narrower leaflets, which rarely exceed 2 cm., and by the presence of small awl-shaped and persistent stipels.

Gymnocladus assamicus U. N. Kanjilal ex P. C. Kanjilal, Assam Forests Rec. Bot. 1: 7, 8. 1934. FIGURE 4.

Trees 5–17 m. tall, the bark yellowish to reddish brown, reticulate. The rachis of the leaves 30–40 cm. long, glabrate to obscurely glandular, with 6–7 pairs of pinnae 11–22.5 cm. long; pinnae 12–14-jugate; leaflets oblong to obovate-oblong, 2–3 × 0.6–1.5 cm., glabrate above, minutely pubescent beneath on the midrib, the apex rounded to obtusely mucronate, the base rounded to cuneate, slightly oblique, the stipel 1, ca. 1 mm. long, awl-shaped, and persistent. Inflorescence racemose, 11–17 cm. long, densely gray, densely pubescent, the bracts and bracteoles minute or absent. Flowers pedicellate, the pedicels ca. 4 mm. long; calyx tube 6–9 mm. long, villous outside, 5-lobed, the lobes 4–6 mm. long, lanceolate to subulate; petals 5, oblong-obovate, 7–9 mm. long, purplish gray; stamens with densely pilose filaments ca. 3 mm. long, the anthers oblong-ovoid; pistil not seen. Fruit oblong, subfalcate, compressed, 14–18 cm. long, 3–4 cm. wide, and 1.5 cm. thick, shortly beaked, with a stalk ca. 8 mm. long, reddish brown, pulp present, the pericarp rather thick, woody,

transversely ridged and grooved (showing the seeds within). Seeds 6–8, obovoid to subglobose, bluntly trigonous, 1.5–2.0 cm. long, 1.2–1.6 cm. wide, with funicles ca. 8 mm. long.

TYPE. India, Assam. Khasi Hills, Laitkseh, 1800 m., *Shillong Herb. no. 7624* (Isotype, SH).

HABITAT AND DISTRIBUTION. This species has hitherto been known only from the type locality in Assam, India. Recent study of Chinese caesalpiniaceous plants, however, shows that a specimen collected in southeastern Yunnan also belongs to this species, suggesting a wider distribution than previously indicated.

ADDITIONAL SPECIMENS. **India.** ASSAM: Khasi Hill, *Shillong Herb. nos. 10157 and 10548* (not seen by the writer). **China.** SE YUNNAN: Mar-li-po, Village of Chung-dzai, in an open "thicket" at the elevation of 1800–1900 m., Nov. 4, 1947, *Feng 12863* (A).

Gymnocladus assamicus is closely related to other Asiatic species of the genus. It is characterized by its more or less falcate fruit, which is transversely ridged and grooved on the surface.

The Khasis use the fleshy pods as a soap substitute for washing their hair.

Gymnocladus burmanicus C. E. Parkinson, Bull. Misc. Inf. Kew 1928: 333. 1928. FIGURE 4.

Trees ca. 17 m. tall, the bark brown with transverse lines. The rachis of the leaves ca. 20 cm. long, shortly and sparsely pubescent to glabrate, usually with 3 pairs of pinnae 8–15 cm. long; pinnae 7–10-jugate; leaflets 4–6 cm. long, 0.5–1.5 cm. wide, the lower ones ovate-lanceolate and oblique, the upper ones lanceolate or nearly so, their bases narrowed, the apex of all leaflets acute to acuminate, with scattered, short, appressed trichomes when young, becoming glabrate in age, the petiolules ca. 2 mm. long, the stipel 1, 1–2 mm. long, awl-shaped, and persistent. Inflorescence ca. 10 cm. long, all the branches shortly and sparsely pubescent. Flowers with pedicel 1–1.3 cm. long; calyx tube ca. 7 mm. long, 5-lobed, the lobes ca. 5 mm. long; petals 5, oblong, pale-pubescent, 8 mm. long, reddish purple; stamens with filaments ca. 7 mm. long, the anthers ovoid; ovary glabrous, few-ovuled, the style short, the stigma slightly oblique. Fruit oblong, subcylindrical, slightly compressed, ca. 8 cm. long, 3 cm. wide, reddish brown, shiny, pulp present. Seeds 2 to 3, oblong-obovoid.

TYPE. Lower Burma, Ta-ok Plateau, Dawna Hill of Tenasserim, at about 1000 m., *Parkinson 5229* (K).

HABITAT AND DISTRIBUTION. This species is known solely from the type collection. According to A. Das (see Kanjilal, 1934), the range of this species extends to adjacent India (Assam); however, no specimen has been recorded from that area.

FIGURE 4. Types of *Gymnocladus assamicus* (left) and *G. burmanicus* (right).

VERNACULAR NAME. Mya-pe-ler (Karen, Lower Burma).

Gymnocladus burmanicus may be separated from other Asiatic species by the narrower, ovate-lanceolate leaflets; the usually larger and reddish purple flowers; and the reddish brown, subcylindrical fruits.

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A REINTERPRETATION OF LEUCAENA AND LYSILOMA

E. A. SHAW AND B. G. SCHUBERT

THERE HAVE BEEN in recent years several papers dealing with the correct names for two species of mimosoid legumes native to the West Indies. The lead tree, or jumbie bean, usually known as *Leucaena glauca* Bentham or "(Willd.) Bentham," is commonly cultivated and widely naturalized both in the Americas and in the Old World. This species is the type of the genus *Leucaena*. The wild tamarind is native to the Bahamas, Cuba, Hispaniola, and southern Florida. This species, the type of the genus *Lysiloma*, is generally called either *Lysiloma latisiliquum* (L.) Bentham or *L. bahamense* Bentham.

There is general agreement that *Leucaena glauca* cannot be used as the name of the lead tree. The whole affair was carefully discussed by De Wit (1961), who pointed out that Bentham's name is based upon "*Acacia glauca* Willd."; nomenclaturally this name represents a transfer to *Acacia* of *Mimosa glauca* L., described in the first edition of *Species Plantarum*. However, Willdenow's description and the specimens in the Willdenow herbarium (IDC 7440. 1389: II. 5, 6, 7, 8, 9) which he annotated as *A. glauca* refer to a species quite different from *Mimosa glauca* of 1753.

The identity of *Mimosa glauca* of 1753 is clear. The name, lectotypified by De Wit (1961) through the choice of a specimen from Adrian van Royen's herbarium at Leiden, is that of an *Acacia*, usually called *A. villosa* (Sw.) Willd., but correctly named *A. glauca* (L.) Moench. However, Linnaeus saw more mimosoid legumes during the next few years, his concept of the species changed, and "*Mimosa glauca*" of the second edition of *Species Plantarum* is not the species of the first edition. In fact, as discussed by De Wit, this second *M. glauca* is the lead tree, as is *Acacia glauca* Willd. One could treat Willdenow's *Acacia glauca* as a new name, but De Wit pointed out that an earlier name for the lead tree already existed. During the eighteenth century this species was cultivated in European botanic gardens, and in 1783 it was described by Lamarck as *Mimosa leucocephala* from a plant in the Jardin du Roi in Paris. The description and the specimens in Lamarck's herbarium (IDC 6207. 204: II. 6, 7) leave no doubt that this is the lead tree; De Wit therefore made the combination *Leucaena leucocephala* (Lam.) De Wit.

However, Gillis and Stearn (1974) have re-examined the matter, and they contend that there is in the first edition of *Species Plantarum* a name for the lead tree, i.e. *Mimosa latisiliqua*, serving as basionym for *Leucaena latisiliqua* (L.) Gillis. This is a drastic change, for this Linnaean name has for a century been applied not to the lead tree but, as *Lysiloma latisiliquum* (L.) Bentham, to the wild tamarind. For the

latter species Gillis and Stearn use the name *Lysiloma bahamense* Bentham.

At the heart of the problem lies the typification of the name *Mimosa latisiliqua*. The protologue of Linnaeus (Sp. Pl. ed. 1. 1: 519. 1753) is:

21. MIMOSA inermis, foliis bipinnatis; partialibus quinquejugis: propriis decemjugis. *latisiliqua.*
Acacia non spinosa, siliquis latis compressis, flore albo.
Plum. spec. 17.
Habitat in America *calidiore.*
Bracteae *dimidiato-cordatae.* Pedunculi *terni*; Flores *capitati.*

In the Linnaean herbarium (LINN) there are three sheets annotated as *M. latisiliqua* and numbered by the late Spencer Savage as 1228.19, 1228.20, and 1228.21 (IDC 177. 716: I. 4, 5, 6, 7). The two latter need not be considered, for each bears the notation by the younger Linnaeus that it was received in 1777. The first sheet, 1228.19, indeed bears a specimen of the lead tree and was annotated by Linnaeus as "21. latisiliqua H. [ortus] U. [psaliensis]" and later by J. E. Smith as "glauca." Gillis and Stearn argue at length that there can be no doubt that Linnaeus had this specimen, taken from a plant cultivated in the garden at Upsala, at hand when he drafted the protologue and that the details of the phrase-name are based upon it; they therefore chose it as lectotype of the name.

They do admit that the specimen on sheet 1228.19 does not agree in all details with the protologue, for the plant has leaves with either five or six pairs of pinnae, not consistently five, and the pinnae have ten to twelve pairs of leaflets, rather than only ten, but they point out that there is variation in these leaf characters and that Linnaeus might have had available other specimens, perhaps from the same tree, or that he, humanly, might have been careless.

The arguments of Gillis and Stearn were put forth in rebuttal to those of De Wit, who in 1961 had typified the name, not by the specimen in the Linnaean herbarium, but by a drawing made by Charles Plumier. The drawings made in the West Indies by Plumier were published only long after his death by Johan Burman of Amsterdam, from 1755 to 1760, as *Plantarum Americanarum Fasciculus . . . continens Plantas, quas olim Carolus Plumierius, Botanicorum Princeps, Detexit, Eruitque, Atque in Insulis Antillis ipse depinxit.* The history of Plumier's drawings and of Burman's publication of them was discussed by Gillis and Stearn (*loc. cit.*)

The drawing published by Burman in 1755 as *tabula sexta* in the first fascicle depicts the wild tamarind and agrees exactly with Linnaeus's phrase-name in that each leaf has five pairs of pinnae and each pinna has ten pairs of leaflets. Could Linnaeus have seen the drawing? No doubt he did, in 1738 in Leiden, for Herman Boerhaave had a set of copies of Plumier's drawings, the "Codex Boerhaavianus," which on Boerhaave's death went to Burman, who eventually published them. Could Linnaeus have remembered one mimosoid legume seen in 1738 when he

drafted *Species Plantarum* during the 1740's, or did he see Burman's plates before their publication?

De Wit maintains that Linnaeus must have done one or the other, for the details of bracts and peduncles in the protologue could have come only from Plumier's drawing. Gillis and Stearn point out that there exists no evidence that Linnaeus made detailed notes when he saw the drawings in 1738, and, moreover, that *M. latisiliqua* does not appear in the 1746–1748 draft copy of *Species Plantarum* in the library of the Linnean Society. They further point out that there is no evidence in Burman's correspondence with Linnaeus that he could have seen this plate before *Species Plantarum* was published. They have therefore typified the name by the specimen in the Linnaean herbarium, and Gillis has made the combination *Leucaena latisiliqua* (L.) Gillis for the lead tree.

It is of some practical importance to determine the correct names for these two species, since each is the type of its genus, and the lead tree is widely grown beyond its natural range and is naturalized in many areas of the Old World tropics, e.g., India, Malaysia, Indonesia, and Australia.

When Bentham described *Leucaena* in 1842, he included the lead tree, as *L. glauca*, and three other species. He described *Lysiloma* in 1844, including the wild tamarind as *L. bahamensis*, and six additional species. The description of *Lysiloma* notes "Stipulae saepius foliaceae v. membranaceae"; that of *Leucaena* says nothing of stipules. It is clear that Bentham intended *Lysiloma* to include species with conspicuous, leaflike stipules. In his "Revision of the Suborder Mimoseae" (1875), Bentham replaced his own earlier name for the wild tamarind with *L. latisiliqua* (L.) Bentham and described the stipules as being leaflike, ovate, acute, and semicordate and auriculate at the base. He also remarked, "Plumier's figure and description, upon which Linnaeus established the species, leaves no doubt as to the identity of his plant with the one above described."

To return to the Linnaean protologue: (1) the phrase-name itself is descriptive of both the specimen in the Linnaean herbarium and of Plumier's drawing, but more exactly so of the latter; (2) Plumier's polynomial from his *Catalogus* (1703) could refer to any one of many mimosoid legumes; but, (3), the details of "bracts" (i.e. stipules) and of peduncles Linnaeus must have had from some source other than the specimen on sheet 1228.19 — the details are exactly descriptive of Plumier's drawing. The protologue is, perhaps, based upon two elements, but one of these surely was Plumier's drawing, and in the interests of nomenclatural stability, it is by this that the name should be typified.

Gillis and Stearn offer in support of their arguments the statement made by Philip Miller in 1759 that Linnaeus's *M. latisiliqua* was the same as the lead tree grown as *Acacia non spinosa, . . . , siliquis longis planis* in the Chelsea Physic Garden. But there is another contemporary comment to be considered. Burman's *Plantarum Americanarum* . . . consists not of illustrations alone. The ten fascicles include 262 pages of text. For each species depicted, there is given in the text the name used by Plumier and the phrase-name from *Species Plantarum* if Linnaeus ac-

cepted the species, as well as synonyms and a short description. The text accompanying *tabula sexta*, the drawing of the wild tamarind, gives Linnaeus's phrase-name for *M. latisiliqua* and a clear reference to its page and number in *Species Plantarum*. Burman, friend and correspondent of Linnaeus, clearly considered Plumier's drawing to represent *M. latisiliqua*.

We regret that we must disagree with Dr. Gillis and Dr. Stearn, but we think that there is very strong evidence that the protologue of *Mimosa latisiliqua* is based, at least in part and likely in its whole, upon Plumier's drawing of the wild tamarind. When and where Linnaeus saw the drawing and thus refreshed his memory of the species we do not know, but the description of "bracteae dimidiato-cordatae" and of "pedunculi terni" did not come from the specimen chosen as lectotype by Gillis and Stearn. Those features he must have seen on the drawing. One cannot now prove that Linnaeus did not see the drawing after 1738 any more than we can prove that he did see it at some later time, but there is no other source for those details about the "bracts," details which indicate that Linnaeus was referring to a species of *Lysiloma*, not to a *Leucaena*. We therefore agree with De Wit that the correct name for the wild tamarind is *Lysiloma latisiliquum* (L.) Bentham, that of the lead tree, *Leucaena leucocephala* (Lam.) de Wit.

There have for many years been controversy and confusion about the correct application of these names, so that much material in herbaria is wrongly named. Furthermore, in the only recent flora for any of the Antilles where the two genera occur, *Flora de Cuba* (Vol. 2, 1951) of Brothers León and Alain, *Lysiloma sabicu* is described as *L. latisiliqua* (L.) Bentham, and the true *Lysiloma latisiliqua* is under the name *L. bahamense* Bentham.

We have studied and examined both literature and the specimens in the herbaria of the Gray Herbarium and the Arnold Arboretum. To aid in clarifying the application of the names we have cited representative specimens of each of the species.

KEY

Pinnae 3–10 pairs; leaflets (9–)13(–20) pairs, acute; stipules lacking or spinescent; flowers usually perfect, each subtended by a peltate bract; stamens 10, free, the anthers versatile, introrse, usually somewhat pilose; pollen shed as single grains; infructescences with several fruits borne from each one, the fruits slender, flat, not coiling; seeds brown and compressed. . . . . *Leucaena leucocephala.*

Pinnae 1–many pairs; leaflets small and numerous or larger and with fewer pairs, petiolar nectary present at least below the lowest pair of pinnae; larger leaflets obovate, obtuse; stipules foliaceous, obovate, or ovate and auriculate; flowers perfect or the lowermost staminate; stamens monadelphous, united for one-fourth to ca. one-half the length of the filaments, the anthers peltate; pollen shed in 16-grained polyads; fruit broad, often twisted at the base, the valves eventually separating from the sutures. . . . . *Lysiloma.*

Pinnae 3–4 pairs; leaflets 3–6 pairs, petiolulate, obovate, obtuse, with second-

ary venation conspicuously reticulate, 1–2.3 cm. long, 0.6–1.5 cm. wide; stipules obovate, ± persistent. ..... *Lysiloma sabicu.*

Pinnae 2–4 pairs; leaflets 11–26 pairs, essentially sessile, elliptic, narrowly obtuse, secondary venation obscure, 0.9–1.5 cm. long, 0.4–0.7 cm. wide; stipules cordate-ovate, auriculate at base, caducous. . *Lysiloma latisiliquum.*

Leucaena leucocephala (Lam.) de Wit, Taxon **10**: 53. 1961.

Mimosa leucocephala Lam. Encycl. Méth. Bot. **1**: 12. 1783. HOLOTYPE: Lamarck herbarium *s. n.* (P).

Acacia leucocephala (Lam.) Link, Enum. Hort. Berol. pars 2. 444. 1822.

Mimosa glauca sensu Linnaeus, Sp. Pl. ed. 2. **2**: 1504. 1763, non *M. glauca* L. Sp. Pl. ed. 1. **1**: 520. 1753 = *Acacia glauca* (L.) Moench, Meth. Pl. 466. 1794 (see De Wit, Taxon **10**: 50–54. 1961; *Ibid.* **24**: 352. 1975).

Acacia glauca sensu Willd. Sp. Pl. **4**: 1075. 1806. The description given by Willdenow is that of *M. glauca* from the second edition of Linnaeus's *Species Plantarum*, but nomenclaturally, the combination is based on *M. glauca* L. of the first edition. = *Acacia glauca* (L.) Moench.

Leucaena glauca "(Willd.)" Bentham, Jour. Bot. **4**: 416. 1842. This combination is based upon "*Acacia glauca* Willd." (see above).

REPRESENTATIVE SPECIMENS from Bermuda, the Bahama Islands, and the Greater and Lesser Antilles. **Bermuda.** Paynter's Vale, *Moore 3133* (A). **Bahama Islands.** NORTH BIMINI: without exact locality, *Howard & Howard 9984* (GH). **Cuba.** Vicinity of Santiago City, *Pollard et al. 287* (A). **Jamaica.** Buff Bay and vicinity, *Mason 10338* (GH). **Dominican Republic.** Guayubin, *Abbott 981a* (GH). **St. Thomas.** Without exact locality, *Eggers 270* (A). **Tortola.** Without exact locality, *Fishlock 177* (A). **St. Kitts.** Without exact locality, *Cooley 8796* (GH). **Dominica.** Morne Bruce, Roseau, *Hodge 613* (GH). **Barbados.** Bridgetown, along sea beach, *Potter 5464* (GH). **Trinidad.** Without exact locality, *Broadway s. n.* (GH).

Lysiloma sabicu Bentham, Hooker's Jour. Bot. Kew Gard. Misc. **6**: 236. 1854. LECTOTYPE: *Sagra s.n.*, "Havanna" (K).

Leucaena formosa Grisebach, Cat. Pl. Cubens. 82 and 284 [addenda] 1866. HOLOTYPE: *Wright 2392* (MA ?), seen in GH.

Acacia formosa sensu A. Richard in Ramon de la Sagra. Hist. de l'île de Cuba. Botanique. Plantes Vasculaires 463. 1845, non *A. formosa* Kunth, Mimoses 102. *t. 32.* 1822 [1819].

REPRESENTATIVE SPECIMENS. **Bahama Islands.** GREAT GUANA CAY: without exact locality, *Britton & Millspaugh 2887* (GH). CAT ISLAND: around Wilson's Bay, *Byrne 253* (A). Without exact locality, *Bryant s. n.* (GH). **Cuba.** Rangel, Rosario Mts., *Bro. Alain 49* (GH); near Blue Beach, 3 miles from Guantanamo, *Fairchild 3887* (A). ISLE OF PINES: Rio Jucaro, *Marie-Victorin & Alain 106* (GH). **Haiti.** Slope of M. Haut de St.-Marc, *Ekman H8080* (GH). **Dominican Republic.** Riverbed of Rio San Juan, Hato del Padre, San Juan, *Ekman H13459* (GH).

Lysiloma latisiliquum (L.) Bentham, Trans. Linn. Soc. London **30**: 534. 1875.

Mimosa latisiliqua L. Sp. Pl. ed. 1. **1**: 519. 1753. LECTOTYPE: *tab. 6* (text,

p. 3), Burman, *Plantarum Americanarum Fasciculus Primus, continens Plantas, quas olim Carolus Plumierius, Botanicorum Princeps, Detexit, Eruitque, Atque in Insulis Antillis ipse depinxit.* 1755.

Acacia latisiliqua (L.) Willd. Sp. Pl. **4:** 1067. 1806.

Lysiloma bahamense Bentham, London Jour. Bot. **3:** 82. 1844. HOLOTYPE: Bahama Islands, *Swainson s.n.* (K).

Acacia bahamensis (Bentham) Grisebach, Fl. Brit. W. Indian Islands 221. 1860.

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA: ca. 1 mile north of Long Pine Key campsite, Everglades National Park, T58S, R36E, *Ward 3933* with *Godfrey & Burch* (GH). **Bahama Islands.** NEW PROVIDENCE: near Nassau, *Curtis 153* (A). RUM CAY: hill overlooking Fort Boyd, *Gillis 6288* (A). MAYAGUANA: Wreck Bay Road, *Gillis & Proctor 11572* (A). **Cuba.** Milpa, Cienfuegos Bay, *Jack 5116* (A); eastern side of entrance to Cienfuegos Bay at Pasa Caballo, opposite Castilla de Jagua, *Wood & Atchison 7444* (A); Guatao, *Bro. León 12473* (GH). **Haiti.** Île la Tortue, between La Vallée & La Roselière, *Ekman H4051* (A); vicinity of La Vallée, Tortue Island, *Leonard & Leonard 15423* (A).

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WOOD ANATOMY OF MYROTHAMNUS FLABELLIFOLIA (MYROTHAMNACEAE) AND THE PROBLEM OF MULTIPERFORATE PERFORATION PLATES

SHERWIN CARLQUIST

THE WOOD ANATOMY of *Myrothamnus flabellifolia* Welw. has been briefly described by Tippo (1938). The purpose of the present study is to expand Tippo's description, to present illustrations of the wood anatomy of this species for the first time, to interpret ecologically the peculiarities of this wood, and to offer some preliminary comments on possible relationships of Myrothamnaceae. The family consists of two species: *M. moschatus* Baillon, of Madagascar, and *M. flabellifolia*, which ranges from Angola and Southwest Africa to the Transvaal (Niedenzu & Engler, 1930; Zemke, 1939). *Myrothamnus moschatus* has never been studied anatomically, and unfortunately material of this species was not available. *Myrothamnus flabellifolia* has been studied for its vegetative anatomy (Grundell, 1933; Zemke, 1939) because of its notable leaves, which expand and contract markedly with water availability. The xeromorphic habit of *M. flabellifolia* may be somewhat deceptive. Although it does grow in winter-dry areas, it tends to occur in crevices of rocky outcrops. Where I observed and collected this shrub in the Magaliesberg just north of Pretoria, Republic of South Africa, the sites it occupied were rock crevices that also proved to be seeps, suggesting attenuated availability of water. Thus *Myrothamnus* can be considered to have both xeric and mesic aspects in its niche preferences, a fact of significance with respect to wood anatomy.

Other features of *Myrothamnus* wood needing explanation include such peculiarities as the type of multiperforate perforation plates, the absence of axial parenchyma, and the nature of the ray histology. Some of these peculiarities may be related to limited accumulation of secondary xylem. Although *M. flabellifolia* is a shrub, stems never become large without splitting into several segments, a habit typical of desert shrubs from various parts of the world. Because secondary xylem accumulation is limited, and because wood anatomy by itself yields restricted data with respect to systematics, the sum of the wood characteristics may not provide much information of use in phylogenetic comparisons. Often the chief dividend of studies in wood anatomy may be an understanding of the ecological and habital characteristics of a species (Carlquist, 1975). Phylogenists can be said to agree generally on the phyletic placement of the Myrothamnaceae, but they differ to various degrees concerning the family's placement in particular orders or its sequence in phylogenies.

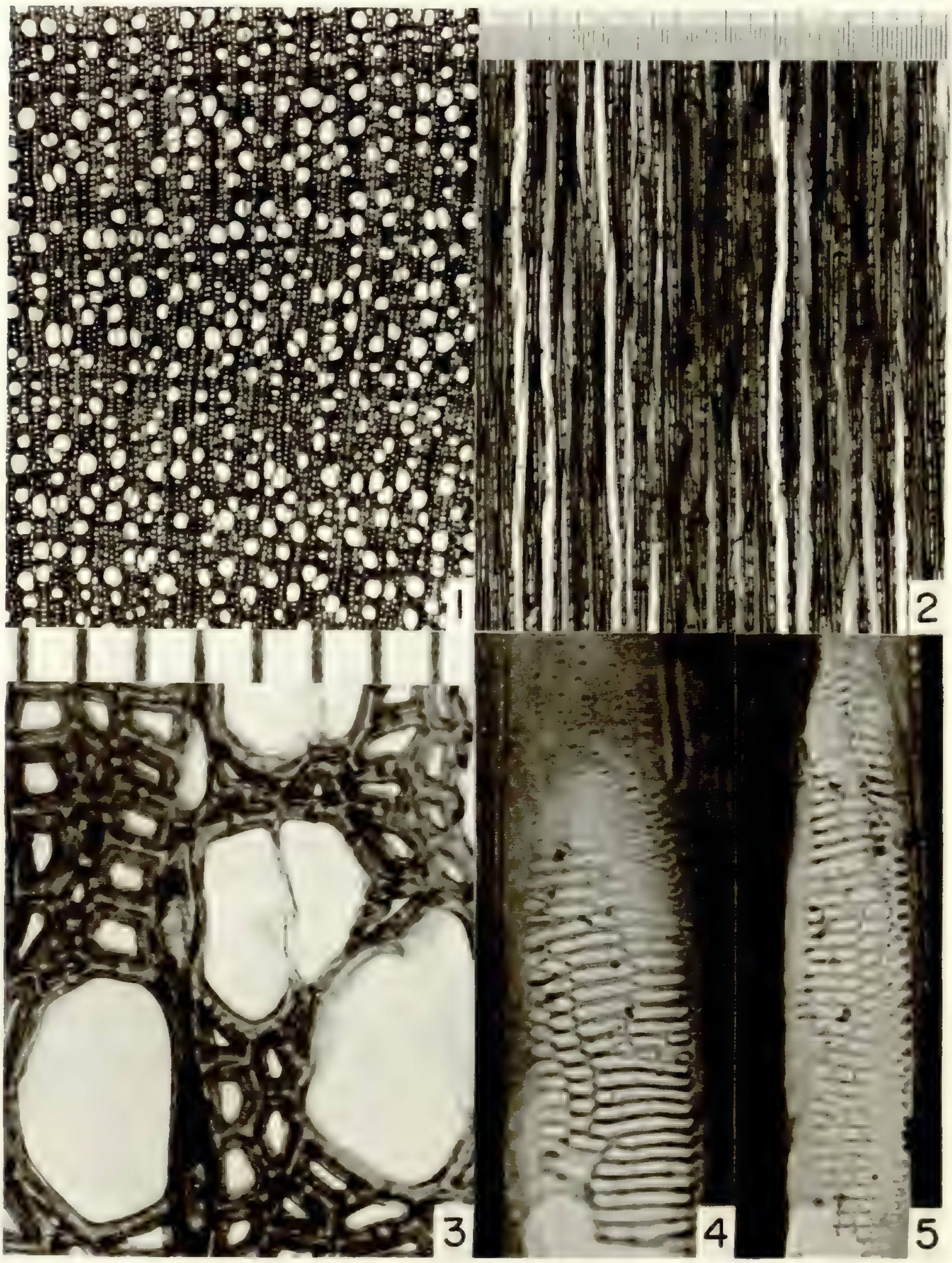
MATERIALS AND METHODS

Wood samples of *Myrothamnus flabellifolia* were collected in the field and dried; the specimen *Carlquist 5133* (RSA, A, and other herbaria) documents this Magaliesberg population. Wood of the largest stem available (ca. 3 cm. in diameter) was sectioned, and the sections were stained with safranin. Macerations were also prepared from this stem, as well as from a large root and a twig, by means of Jeffrey's fluid; a safranin stain was used. Unfortunately, circumstances did not permit liquid preservation of wood samples, a procedure desirable in view of the possible nucleated nature of tracheids. For quantitative data, 50 measurements per feature were obtained.

ANATOMICAL OBSERVATIONS

Description. The following description is based on stem material, with data from the root and twig samples added where noted.

Woody cylinder furrowed at periphery. Growth rings inconspicuous (FIGURE 1) but definitely present. Vessels mostly solitary (FIGURE 1), the average number of vessels per group 1.05. Mean vessel diameter 36 μm. Mean vessel-element length 534 μm. in stem, 621 μm. in twig, 613 μm. in root. Vessels angular in transectional outline (FIGURE 3). Perforation plates of a modified scalariform type (FIGURES 4 & 5), somewhat reminiscent of radially very much widened pits and thus networklike, sometimes with thin strands of wall material interconnecting the bars (FIGURE 5). Range and average number of bars not determinable because of the networklike pattern. Bars at least sometimes with inconspicuous vestigial borders. Lateral wall pits of vessels circular in outline (FIGURE 4, above), sometimes opposite but elsewhere so sparse that the pattern cannot be termed alternate or opposite. All imperforate elements tracheids, with pits fully bordered and apertures circular to elliptical, the longest axis still shorter than the diameter of the pit cavity. Apertures sometimes appearing to lengthen by the fracturing of the apparently gelatinous inner secondary wall. Marked shrinkage patterns indicative of gelatinous nature of tracheids not evident, but staining reactions (FIGURE 3) of inner secondary wall layers different from those of outer layers. Tracheids often rectangular in transectional outline (FIGURE 1; FIGURE 3, upper left), tangentially up to twice as wide as radially (often 16 μm. $\times$ 9 μm. or 16 μm. $\times$ 8 μm.). Pits in more than a single series on the walls that are tangentially widened. Mean tracheid length in stem 533 μm.; in twig 633 μm.; in root 655 μm. Mean tracheid-wall thickness 2.3 μm. Axial parenchyma absent. Rays exclusively uniseriate (FIGURE 2), composed mostly of erect cells, with a few square cells and virtually no procumbent cells (if present, only slightly wider radially than vertically). Mean ray height 427 μm. Crystals absent. Amorphous deposits (tending to appear threadlike or webby) present in ray cells and tracheids; presence of such deposits uniform in both ray cells and tracheids,



FIGURES 1–5. Wood sections of *Myrothamnus flabellifolia*: 1. transection. showing numerous but inconspicuous growth rings; 2. tangential section — note numerous uniseriate rays; 3. portion of transection, the walls of tracheids showing darker-staining inner wall layer; 4 & 5. portions of perforation plates from radial sections: 4, sparse lateral-wall pitting visible above perforation plate; 5, perforation plate with tenuous interconnections of strands between bars. Magnifications indicated by photographs of stage micrometer enlarged at same scale as applicable figures: 1 & 2, scale above FIGURE 2 (finest divisions = 10 μm.); 3–5, scale above FIGURE 3 (divisions = 10 μm.).

suggesting that tracheids may have a longevity like that of ray cells and may therefore be nucleated.

Element length. Tippo (1938) found the mean vessel-element length in his material to be 905 μm., which is appreciably longer than the mean in my material. The provenance of Tippo's specimen is not reported, but different populations and different portions of a plant can easily yield differences in element length of this magnitude.

The ratio of mean tracheid length to mean vessel-element length for any given wood sample is of interest, for ratios only a little greater than 1.00 indicate the primitiveness of a wood (a sort of measure of minimal differentiation between mechanical and conductive systems in wood), while ratios may range as high as 8.00 in specialized woods (Carlquist, 1975). In my data above, the ratio would be 0.99 in the stem, 1.07 in the root, and 1.02 in the twig. That vessel elements should on the average be shorter than tracheids in a given wood sample is an anomaly seemingly contrary to the commonly held notion that imperforate elements are at least a little longer than the vessel elements they accompany. I have noted (1975) an exception to the low ratio as indicator of primitiveness in *Leitneria floridana*, which has specialized wood with libriform fibers only slightly longer than vessel elements. This I ascribed to the limited stem size in *Leitneria*, in that mechanical elements, which tend to be stronger when longer (for a discussion, see Carlquist, 1975), would be of lessened selective value for length. Cumbie (1967) has, in fact, reported circumstantial evidence of limited intrusiveness of libriform fibers during maturation in *Leitneria*. Except in the stem of *M. flabellifolia*, the only other instance I know in which the tracheid-to-vessel element length ratio falls below 1.00 is in the stem of *Grubbia rosmarinifolia* (unpublished data); this species is also a small shrub of finite size. While one might say that in these two instances a ratio below 1.00 is an anomaly due to insufficient number of measurements and that a ratio of 1.00 or more would be obtained had more cells been measured, there is another possibility. In these two species, as well as in *Leitneria floridana*, finite stem size may well be related to lack of intrusiveness of imperforate elements, for reasons cited above. At the same time, the enlargement of vessel elements in diameter during their maturation might have, as an inevitable component, a tendency toward intrusiveness in length also. One must remember that our knowledge of wood anatomy in shrubby and herbaceous species is still rudimentary compared with the data on hand concerning the wood of tree species. However, I would interpret the low ratios in *M. flabellifolia* to be indicative of primitiveness, because they are associated with morphological primitiveness of both tracheids and vessel elements.

Rays. Tippo (1938) described rays of his material of *Myrothamnus flabellifolia* as corresponding to Kribs's "Heterogeneous Type 3," that is, uniseriate rays present exclusively and these composed of procumbent,

square, and erect ray cells. If procumbent cells were lacking or nearly so, as I found in my material, these rays would not fall into any of the categories of Kribs (1935). In fact, rays composed solely of square and erect cells, or of erect cells only, can be found in a number of dicotyledons with limited secondary xylem accumulation. A hypothesis for the possible functional significance of such rays has been given elsewhere (Carlquist, 1962, 1975, 1976b) and is mentioned below in relation to axial parenchyma.

Axial parenchyma. The absence of axial parenchyma in *Myrothamnus flabellifolia* might be explained in two ways. First, the abundance of uniseriate rays (FIGURE 1), with ray cells predominantly erect, may represent a tissue that functions both in vertical and radial horizontal conduction and in storage of photosynthates. This condition would be expected more in stems with small size, and therefore little radial conduction, than in large stems, where procumbent cells would improve radial conduction (Carlquist, 1975). A second possible explanation might be that tracheids in *M. flabellifolia* may have greater than normal longevity and, as nucleated cells, function like axial parenchyma in conduction and storage (see Wolkinger, 1969 & 1970, and Carlquist, 1975, for data and discussions). A number (but by no means all) of the dicotyledons that lack axial parenchyma have limited secondary xylem accumulation. However, the correlation between the absence of axial parenchyma and the nucleated nature of imperforate elements is nearly perfect.

Perforation plates. In *Myrothamnus flabellifolia*, Tippo (1938) claimed that "all the perforation plates are scalariform. There are many bars (about 45) and the perforations are narrow." My data differ somewhat, for I found perforation plates to be relatively wide and easily distinguished (FIGURES 4 & 5), with fewer than 45 bars, if bars can be distinguished where plates are rather networklike. Some perforation plates in my material were superficially scalariform, but even in these plates strands of secondary wall material interconnecting the bars could be seen. More commonly, the perforation plates appeared to consist of two or three series of perforations (FIGURE 4), as though alternate pits without membranes were widened radially into perforations. Such perforation plates have been figured by Jane (1956) for *Vaccinium leschenaultii* and by Wilson (1960) for *Warburgia ugandensis*, *Cinnamosma madagascariensis*, and *Canella alba*. The type of perforation plate with strands irregularly interconnecting the bars has been figured by Carlquist (1961b) for *Carpenteria californica*, by Solereder (1908) for *Epacris heteronema*, and by Wilson (1960) for *Warburgia stuhlmanii*. Multiperforate perforation plates with variously random arrangement of bars and openings, unlike those of *Myrothamnus*, have been figured by a number of authors, such as Butterfield and Meylan (1975), Carlquist (1956a, 1961a, 1976a), Chalk (1933), Gottwald and Parameswaran (1964), MacDuffie (1921), and Parameswaran and Liese (1973). Such perforation plates may, in a few cases, be simplifications of the perforation plate related to the vin-

ing habit, as in the Bignoniaceae or in *Tetracera* (Dickison, 1967), or they may be based on metaxylem perforation plate patterns, as figured for the metaxylem of various dicotyledons by Bierhorst and Zamora (1965). Irregular presence of multiperforate plates in secondary xylem may characterize some families of a predominantly herbaceous nature, such as the Asteraceae, in which the secondary xylem may contain more metaxylem characteristics than in exclusively arborescent families.

The type of multiperforate plate in which irregular interconnections between bars occur (and this may be construed to include the *Myrothamnus* type) may have a functional significance. As I (1975) hypothesized in the case of "Langsbälchkenstrukturen" crossing pits in scalariformly pitted tracheids of *Sigillaria* (figured by Henes, 1959), a form of strengthening, representing a phylogenetic innovation and not a relictual phenomenon, may have been evolved. One can hypothesize that in dicotyledons with primitive wood structure most have adapted to seasonal water availability through simplification of the perforation plate to fewer bars (Carlquist, 1975). However, in other cases, strengthening of the scalariform perforation plate by innovation of strands that interconnect the bars may have evolved as a mechanism for accommodation of high tensions in the xylem during dry seasons. This would be understandable if slow rates of conduction also occurred, for narrowing of the total perforation area would be selectively tolerable only with slow conductive rates. Such slow rates can be achieved by means such as heavy cuticularization of leaves (as in *Carpenteria californica*), reduction in leaf size (as in *Myrothamnus*), or both reduction in leaf size and alteration in leaf surfaces to reduce transpiration (as in *Roridula dentata*, Carlquist, 1976a). Thus, a few plants with scalariform perforation plates of an altered type may persist in areas of seasonal dryness. This hypothesis was also employed to explain the fact that multiperforate perforation plates are present in vessels of *Ephedra*, while *Gnetum* (with large leaves and presumptively occasionally rapid rates of transpiration) almost always has simple perforation plates (Carlquist, 1975).

SYSTEMATIC RELATIONSHIPS

Wood anatomy alone can offer only a limited amount of relevant information. Tippo (1938) claimed that *Myrothamnus* resembles Hamamelidaceae very closely with respect to wood anatomy. This is in a sense true, although Hamamelidaceae differ in their heterogeneous multiseriate rays and in their possession of axial parenchyma. The family Myrothamnaceae has been placed in the Hamamelidales by a number of authors (e.g., Cronquist, 1968; Hutchinson, 1959), a position not very different from its placement in the Rosales in other systems (e.g., Wettstein, 1935). Thorne (1968) included Myrothamnaceae in his order Pittosporales, the composition of which represents one of Thorne's bolder innovations. Thus *Myrothamnus* can be considered generally "rosoid" according to all the authors cited. *Myrothamnus* could be compared

closely in wood anatomy to families other than the Hamamelidaceae. For example, the wood of Roridulaceae differs only in the presence of axial parenchyma and a few very minor details (Carlquist, 1976a). Therefore, although wood anatomy confirms a "rosoid" position for *Myrothamnus*, other lines of evidence are required for formulation of a more precise statement of familial relationships. Wood anatomy does clearly mark *Myrothamnus* as one of the few relictual groups that have retained primitive xylem in pockets of mesic habitat within southern Africa. Other such families include the Bruniaceae, Canellaceae, Cornaceae (*Curtisia*), Geissolomataceae, Grubbiaceae, and Roridulaceae. The compensatory mechanisms by which such groups, even in mesic microclimates, have proved adaptive despite primitive types of conducting tissue form an interesting topic in ecological anatomy, which I have sketched in an earlier book (Carlquist, 1975, pp. 149–150).

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COVER: A "mass collection" of leaves of *Sassafras albidum* (Nutt.) C. G. Nees, a handsome lauraceous tree of eastern North America and a probable Arcto-Tertiary relict, along with its two living congeners in eastern Asia. Its attractive small, yellow flowers are produced early in the spring as the leaves first unfold. The elliptic leaves, either entire, mitten-shaped, or 3-lobed at apex, become beautifully red-and-yellow colored in autumn. Although sassafras has long been thought to have medicinal properties, it is probably no more than a mild aromatic stimulant. A tea is made from the wood of sassafras roots; from its leaves, which contain ethereal oil and mucilage cells, gumbo filé, a powder used to give flavor and consistency to gumbo soup, is prepared. Karen S. Vanhoy, whose original illustrations were used on the two preceding covers, also planned and executed this one, as well as the designs and devices in other parts of the Journal and on the offprint covers.

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A REVISION OF THE GENUS KOELREUTERIA (SAPINDACEAE)

F. G. MEYER

IN HIS REVISION, published posthumously in *Das Pflanzenreich* (1933), L. Radlkofer recognized seven species of *Koelreuteria* Laxmann, all from eastern Asia. Among the 143 genera and 14 tribes of Sapindaceae delimited by Radlkofer, the tribe Koelreuterieae consists of *Koelreuteria*, *Stocksia*, and *Erythrophysa*, all of the Old World (Radlkofer, 1931). Its immediate relationships are with tribe Cupanieae (45 genera), tribe Cossignieae (two genera), and tribe Dodonaeeae (14 genera).

Radlkofer was the acknowledged world authority on the Sapindaceae, and his monumental world monograph of the family (1931–1934) is still the standard reference. While the treatment of *Koelreuteria* reflects the author's characteristic scholarly resumé of the literature and related historic details, the taxonomic portion suffers from a rather limited understanding of relationships and variation within the group, due, no doubt, to a paucity of available material for comparison. In the writer's view, too many taxa were recognized at the species level, causing problems in the application of names to these trees both in the herbarium and in cultivation. Two members of the genus, *K. bipinnata* (syn. *K. integrifoliola*) and *K. elegans* (syn. *K. henryi*, *K. formosana*) have been the source of most of the taxonomic confusion existing among botanists, horticulturists, and others who have dealt with these trees in the past. The third member, *K. paniculata*, is much less troublesome taxonomically. All of the known species of *Koelreuteria* are trees of widely recognized horticultural merit; they are found in parks, arboretums, campuses, nurseries, and gardens of this country and of many other countries as well. A critical review of the genus, therefore, has been undertaken to update the taxonomy of the group, especially with reference to the cultivated members.

Since Radlkofer's day, a vast quantity of new material has become available, and the known distribution of the genus has been extended from Taiwan to Fiji, some 7200 km. to the southeast. As currently recognized, the genus *Koelreuteria* consists of three entities at the species level, *K. paniculata* and *K. bipinnata*, both confined to China, and *K. elegans*, distributed in Taiwan and Fiji. Evidence now shows conclusively

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that *K. paniculata* is not indigenous to Korea and Japan, as hitherto recorded by some authors, but occurs in those areas only as a naturalized introduction dating from an earlier period in history.

The plant described as *Koelreuteria minor* Hemsley (1900) has been removed from the genus *Koelreuteria*. It will be treated separately as a proposed new genus on the basis of distinctive floral characters which heretofore have not been recognized.

This account is based on material borrowed from 35 herbaria, as well as on personal observations of living material of all the taxa presently in cultivation.

HISTORY

The genus *Koelreuteria* dates from 1772 and was based on cultivated material grown at St. Petersburg (now Leningrad). Earlier, during his 14-year sojourn in north China, the Jesuit father Pierre d'Incarville (1706–1757) sent seeds of many different plants to a Professor Krashenninikov, academician botanist at St. Petersburg, and to Bernard de Jussieu in Paris. He also made the first herbarium collection of north Chinese plants, which is still preserved in the Muséum National d'Histoire Naturelle in Paris. In addition to seeds of *K. paniculata*, D'Incarville also sent seeds of a number of woody plants previously unknown in Europe, including *Ailanthus altissima*, *Biota orientalis*, *Caragana chamlagu*, *Gleditsia sinensis*, *Lycium chinense*, *Vitex negundo*, and *Zizyphus jujube* (Bretschneider, 1881).

The tree now called *Koelreuteria* was first observed by Erik Laxmann (1737–1796) [1] growing in the winter gardens of the Academy in St. Petersburg, where it flowered for the first time in the warm summer of 1771. Laxmann, in his admiration for the plant, sent a leaf and a brief Latin description of the tree to Linnaeus in a letter dated August 5, 1771; the letter is still preserved in the Linnean Society in London. Laxmann's enthusiasm was later transmitted in Novi Commentarii Academiae Scientiarum Imperialis Petropolitanae **16**: 561. 1772, the publication in which the name *Koelreuteria* appears for the first time. His introductory comments are as follows (from the Latin):

> "Although for 20 years and more this little tree has flourished in the winter gardens of the Academy, yet no one could classify it exactly, lacking any fruiting all these years. The earlier part of the past summer [1771], I mean the months of May and June, which were quite

[1] Laxmann, of Finnish birth, attended botanical lectures by Pehr Kalm, famed pupil of Linnaeus and botanical traveler in North America, at the University of Åbo (now Turku) in Finland. In 1762 he moved to St. Petersburg; he later made extensive travels across Siberia and once visited Alaska, then a Russian province. He corresponded with Linnaeus between 1764 and 1776 and published 5 botanical papers, in addition to pursuing his other interests in mineralogy, chemistry, travel, and entomology. He died during the middle of a Siberian winter in 1796 on his way to Japan (cf. Raskin & Shaffranovskii, 1971).

moist, were so favorable to flowering that the *Arachis hypogaea*, and other plants native to the tropics, not only joyfully bloomed in the windows of my greenhouse, but even matured fruits. Also adorned with flowers was this little tree, whose nuptials our botanist had for so many years eagerly awaited. And so it was my fortune, to my exceeding delight, to be a spectator at these very rare nuptials. Having seen the flowers, I have taken care to depict from life this small tree, which constitutes its own genus. And in order to offer some small token of my esteem, and that of the world of plant lovers, to a man outstandingly and deservedly most distinguished, both in botany and in our botanic garden, Koelreuter,[2] I have named it *Koelreuteria*."

The genus has been treated by various authors. Jussieu (1789) was the first to associate *Koelreuteria* (misspelled "*Kolreuteria*") with the plant family "Sapindi"; De Candolle (1824) placed *Koelreuteria* among four genera of Sapindaceae, Tribe III, Dodonaeaceae H.B.K.; and Bentham and Hooker (1862) placed the genus among 89 genera in Suborder 1. Sapindeae of the Sapindaceae.

The taxonomic investigations of Sapindaceae by Radlkofer (who lived from 1829 to 1927), including revisions of all the genera, covered nearly half a century and are the most comprehensive ever undertaken of the family as a whole.

In his world monograph of the family in *Das Pflanzenreich* (1931–1934), Radlkofer placed *Koelreuteria* in his subfamily Dyssapindaceae (Sapindaceae anomospermae) in tribe Koelreuterieae Agardh (see Agardh, 1858) with two other genera, distinguishing between them as follows (from the German):

A. Trees with large pinnate to bipinnate leaves with a naked rachis; flowers medium-sized, yellow; sepals valvate. ..... *Koelreuteria* Laxm.
A. Shrubs with small leaves; sepals imbricate.
  B. Thorny shrubs with simple leaves, the membranous capsule 3-lobed. ..... *Stocksia* Bentham.
  B. Unarmed shrubs with pinnate leaves and a winged rachis, the utriclelike membranous capsule ultimately irregularly dehiscent. ..... *Erythrophysa* E. Meyer.

MORPHOLOGY AND TAXONOMIC CRITERIA

HABIT. The genus *Koelreuteria* consists of medium-sized to large deciduous trees, usually with thick, rough to furrowed bark. Lenticels normally occur, especially on the twigs and young branches, although they are not diagnostic at the species level.

VEGETATIVE SHOOTS. Normally the terminal shoot bud remains permanently dormant. Growth usually emerges from axillary leaf buds below the

[2] Joseph Gottlieb Koelreuter (1733–1806) was a professor of natural history and director of the Margrave's gardens at the University of Karlsruhe. Koelreuter's fame rests as the first plant hybridist.

shoot apex. In *Koelreuteria paniculata*, for example, the dormant terminal vegetative buds may persist for several years, giving a characteristic knobby appearance to the twigs. The ontogeny of the two outer prophylls or bud scales of each axillary leaf bud may be compared with that of the lateral prophylls found in certain species of *Carya* (Stone, 1962).

LEAVES. The compound leaves are alternate and characteristically imparipinnate. Good taxonomic differences are exhibited in the leaves, and it is possible much of the time to distinguish the species on the basis of leaf differences.

INFLORESCENCES. Radlkofer (1933) referred to the ultimate flowering branches as "thyrsoideis cincinnigeris," whereas Baillon (1878) referred to the same structures as "terminal ramosely cymiferous racemes." Modifications that resemble a cyme may occur, but basically the inflorescence of *Koelreuteria* is indeterminate and racemose and, in this respect, similar to some other sapindaceous genera, such as *Sapindus* and *Cupania*.

FLOWERS. (FIGURES 9, 12, 13.) Polygamy is the usual condition found in *Koelreuteria*. Normally, the flowers are functionally unisexual, both staminate and carpellate flowers occurring together in the same ultimate tertiary or quaternary branchlet. In the first flush of flowering, staminate flowers predominate in a ratio of approximately two staminate to one carpellate, although as flowering progresses carpellate flowers may predominate. Clos (1869) first observed that flowers of *Koelreuteria* produce stamens of two lengths, "les longistaminées," with functional stamens in wholly staminate flowers, and "les brevistaminées," with short erect and nonfunctional stamens in carpellate flowers. Although the anthers in carpellate flowers fail to develop properly and soon abort, further observation shows that the pollen grains are usually normal in size. As observed in *K. paniculata* and *K. elegans* subsp. *formosana*, the flowers are entomophilous, bees and other small insects being the usual pollinators.

At anthesis, the flowers of *Koelreuteria* are asymmetric, a condition derived through a shift of the petal and staminal whorls during growth. While in early bud stage both the petal and stamen whorls are regular and concentric, during development the petal limbs become reflexed in a posterior position and the staminal whorl becomes declinate through a shift in position of the filaments.

Petal shape in combination with other characters is of some diagnostic value in the identification of the taxa. Each petal consists of a claw (stalk) and limb with two accessory appendages. The appendages have been variously interpreted as "nectarium squama" (Laxmann, 1772), as "appendices glanduliformes" (Payer, 1857), as "bipartite scales" (Baillon, 1878, and Radlkofer, 1931), and as "glands" (Elwes & Henry, 1913). These accessory organs are, in fact, thickened lobulate-undulate outgrowths of the petal limb, whose function is undoubtedly the attraction of bees and other pollinating insects. In fresh, young, opening flowers of *Koelreuteria paniculata* and *K. elegans* subsp. *formosana*, for example,

the appendages appear uniformly yellow, the same color as the petal limb, while at anthesis, when various pollinators appear, the appendages turn a bright orange-red. Dr. Frank S. Santamour, research geneticist at the U. S. National Arboretum, has identified the red anthocyanin pigment in the appendages of *K. paniculata* as cyanidin 3-rutinoside, a fairly common pigment among flowering plants. The flowers, also, are quite fragrant in both species observed. Fresh flowers of *K. bipinnata* were not available for study.

Clos (1869) referred to the short raised stalk between the calyx and the disc as the androgynophore.

FRUIT. The dry, winglike papyraceous capsules provide an important means of identification, particularly in *Koelreuteria paniculata*, which has tapering conoidal capsules and is clearly distinguished from *K. bipinnata* and *K. elegans*, both with suborbicular to rotund capsules and morpho-

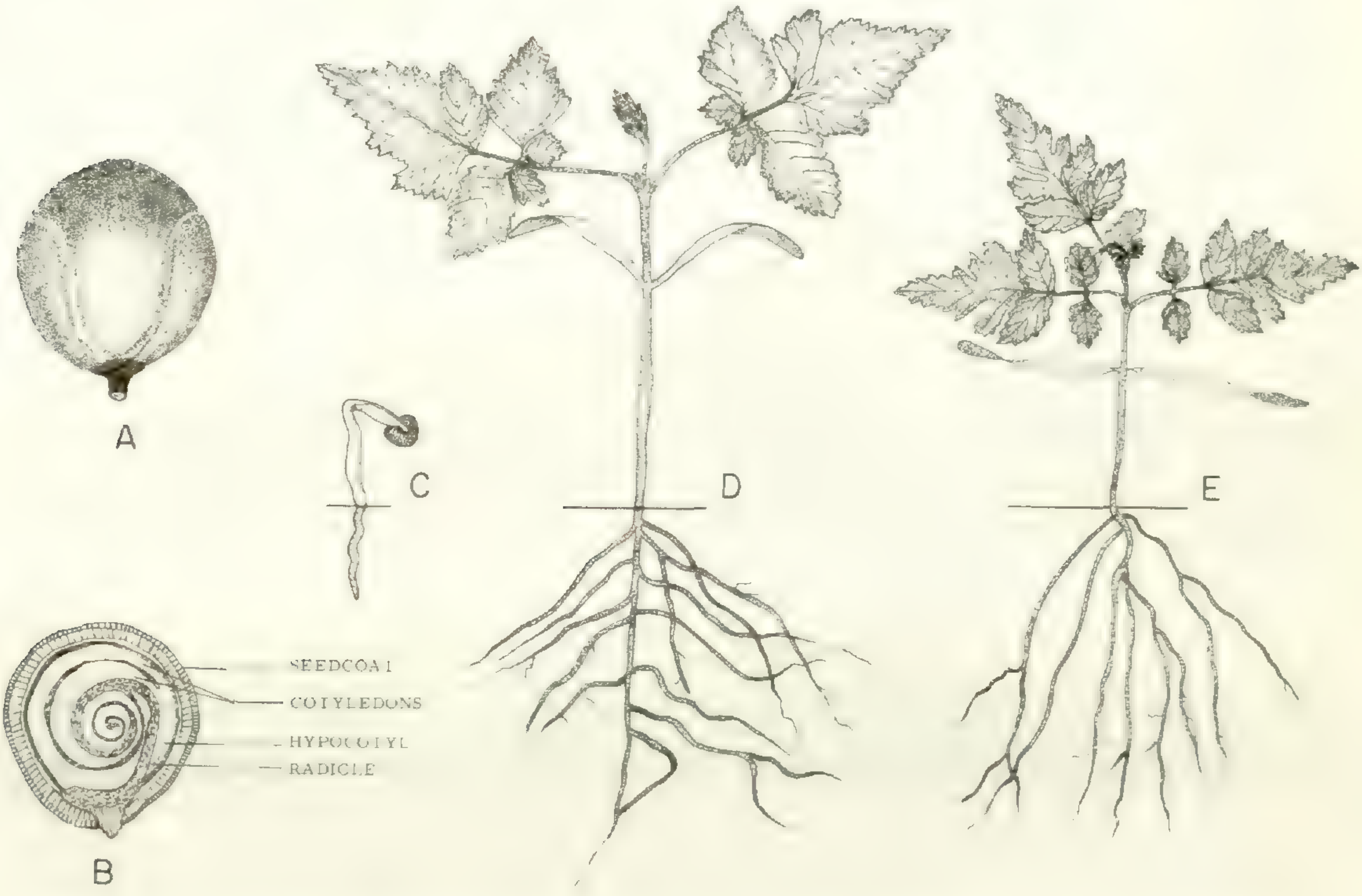


FIGURE 1. A–D, *Koelreuteria paniculata*: A, seed showing U-shaped outline of radicle on surface, × 2½; B, longitudinal section of seed, according to Rudolf (1974); C, germinating seed, first day, × ⅓; D, first pair of true leaves already resemble the mature leaves, × ⅓. E, *K. bipinnata*, showing first true leaves still in juvenile condition, × ⅓.

logically very similar. In the past, too much emphasis has been placed on fruit characters, causing some of the confusion in the taxonomy of *Koelreuteria*. On the basis of fruit alone, Hemsley in 1900 described a plant as *K. minor*, with small retuse capsules, and Radlkofer (1933) followed a similar course in dealing with the same plant. Now that flowers are

available, it is clear that *K. minor* belongs not to the genus *Koelreuteria* at all, but to a new genus soon to be described.

SEEDS AND SEEDLINGS. (FIGURE 1.) The seeds are hard and smooth, with a bony seed coat, and they vary in size and shape from subspherical to pyriform. The persistent funiculus forms a short stipe at the base of the seed, which is diagnostic for the genus.

The seeds of *Koelreuteria* are difficult to germinate because of the bony seed coat. According to Rudolf (1974), dormancy and delayed seed germination may be overcome when the hard, impervious seeds are first soaked in sulfuric acid for one hour and then stratified in moist sand for 90 days at 41° F. (5° C.). Mechanical scarification also promotes fairly rapid germination. Seeds of *K. paniculata* may remain viable over a reasonably long period of time, with a 50 per cent germination recorded after ten years of storage in an unsealed glass jar.

The cotyledons in all of the species are strap-shaped. Of interest is the transition to mature leaves which takes place with the appearance of the first true leaves in *K. paniculata*. In *K. bipinnata* and *K. elegans* the first true leaves are strongly serrate, a condition of juvenility that persists during the early life of the plant before the mature leaves appear; data on the length of the transitional period, however, is lacking.

CHROMOSOMES. Darlington and Wylie (1955) reported a base number of $x = 11$ for the sapindaceous genera *Cardiospermum* and *Koelreuteria*. Bowden (1945) reported a chromosome count of $2n = 22$ for both *K. paniculata* and *K. elegans* subsp. *formosana* (*K. formosana*). A count of $2n = 30$ for *K. paniculata* was reported by Eichhorn and Franquet (1936) but may be inaccurate.

POLLEN MORPHOLOGY

The following discussion of pollen morphology was contributed by Dr. Joan Nowicke, palynologist, Smithsonian Institution, Washington, D. C.

MATERIALS AND METHODS. Pollen samples were removed from herbarium specimens, acetolyzed according to the method outlined by Erdtman (1966), and mounted in glycerin jelly. All slides are deposited at the Pollen Laboratory, Department of Botany, Smithsonian Institution. Measurements are based on only 10 grains and should, therefore, be treated with reservation. Material for the scanning electron microscope was acetolyzed and mounted in a mixture of alcohol-water. After evaporation, the grains were vacuum-coated with gold, examined, and photographed with a Cambridge Stereoscan MK II A microscope.

GENERIC DESCRIPTION OF POLLEN. Grains single, spheroidal, oblate-spheroidal or rarely prolate-spheroidal, 20–27 μm. P × 21–27 μm. E, the amb (polar view) triangular, 3-colporate, the apertures at the angles (angulaperturate), the exine ca. 1.5–2 μm. thick (measured at the poles),

the ektexine finely striate, the striae parallel or irregular and finely striate-reticulate. (FIGURES 2–7.)

The pollen grains of the four taxa examined were very similar and, with the exception of *K. elegans* subsp. *elegans* from Fiji, almost identical. Descriptions of pollen are given below for three species: *K. paniculata* Laxm., *K. bipinnata* Franchet, and *K. elegans* (Seem.) A. C. Sm.

Koelreuteria paniculata Laxm. FIGURES 2, 3.

Grains subprolate to spheroidal, 25–27 μm. P × 21 μm. E, the exine ca. 1.5–2 μm., the ektexine striate.

MATERIAL EXAMINED. **China.** Litang valley, Muli Dist. [28.20N, 100.48E], 10000–11000 ft. alt., *Forrest 21330* (US).

Koelreuteria bipinnata Franchet. FIGURES 4, 5.

Grains oblate-spheroidal, 22–23(–26) μm. P × 23–27 μm. E, the exine ca. 2 μm., the ektexine finely striate.

MATERIAL EXAMINED. **China.** Ta-long-tan, près Tapin-tze, 21 juillet 1886, *Delavay s.n.* (P).

Koelreuteria elegans (Seem.) A. C. Sm. subsp. **elegans**. FIGURES 6, 7.

Grains mostly spheroidal, 24–26 μm. P × 24–26 μm. E, the exine ca. 1.5 μm., the ektexine finely striate-reticulate.

MATERIAL EXAMINED. **Fiji.** Nadroga & Novosa, Nabosewale, vicinity of Nadrau, (*Ranamu*) *Fiji Dept. For. 1171* (SUVA).

This is the most distinctive pollen of the four taxa examined because of the irregularly striate ektexine.

Koelreuteria elegans subsp. **formosana** (Hayata) F. G. Meyer.

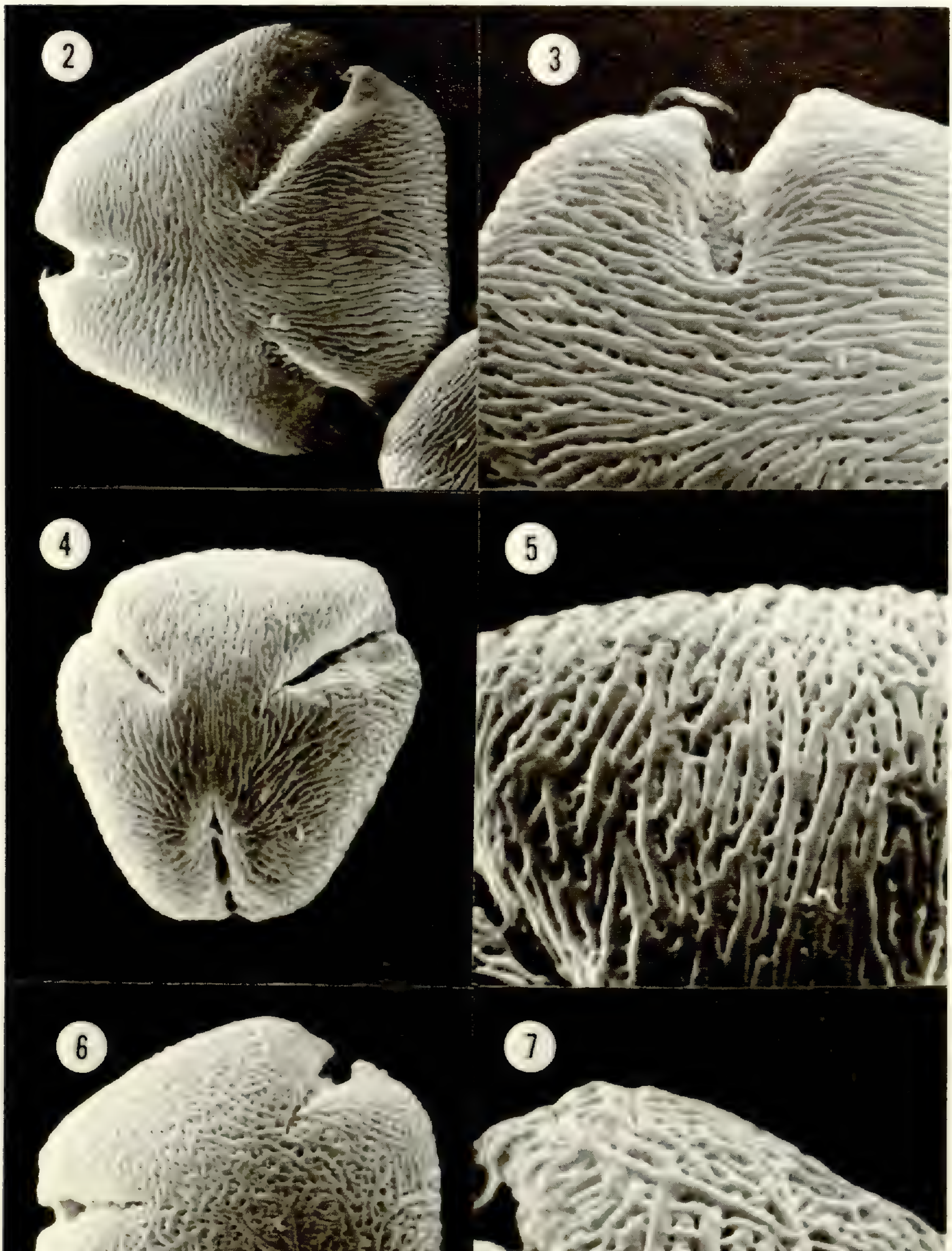
Grains mostly spheroidal, 20–23 μm. P × 21–23 μm. E, the exine ca. 1.5 μm., the ektexine striate.

MATERIAL EXAMINED. **Taiwan.** Cuntin Hunchuen, *Keng s.n.* (US).

This subspecies is very similar to *K. bipinnata*.

ACKNOWLEDGMENTS

I should like to thank the curators of all 35 herbaria for the loan of valuable herbarium material which made the present study possible. In addition, many individuals have given inspiration and encouragement. Initially, John M. Fogg, Jr., and the late Sigmond L. Solymosy pointed out the need for a thorough study of the cultivated members of the genus *Koelreuteria*. I am also indebted to the following persons for specimens and for the variety of ways in which they were helpful: Dr. Le-min Chang,



FIGURES 2–7. Scanning Electron Micrographs of *Koelreuteria* pollen: 2, *K. paniculata*, polar view, × ca. 2035; 3, *K. paniculata*, enlargement of surface

Dr. Francis Ching, Dr. John R. Creech, Mr. Leonid Enari, Mrs. Bruce English, Prof. Joseph Ewan, Dr. Charles R. Gunn, Dr. Hiroshi Hara, Dr. Shiu-ying Hu, Dr. Hiroo Kanai, Ms. N. Khan, Dr. Yong No Lee, Mr. William U. Massey, Dr. Katherine K. Muller, Mr. John Popenoe, The Earl of Rosse, Dr. Frank S. Santamour, Mr. Paul W. Soderholm, Mrs. S. Swatibau, Professor Vivi Täckholm, and Ms. Saula Vodonaivalu. For translations I am indebted to Mrs. Elaine Mathers (Latin), Dr. Elmer E. Leppik (Russian), and Mrs. Evelyn Chen (Chinese). Mr. T. O'Grady, Secretary of the Linnean Society, London, sent valuable manuscript data, and I am equally indebted to Dr. W. T. Stearn of the British Museum (Natural History) for supplying details from the Laxmann correspondence in the Linnean Society. Dr. Joan Nowicke has kindly contributed the details on the pollen and furnished the scanning electron microscope photographs. Finally, I am greatly indebted to my wife Lillian for her continued encouragement and for the drawings that embellish these pages.

TAXONOMIC TREATMENT [3]

Koelreuteria [4] Laxm. in Nov. Comm. Acad. Sci. Imp. Petrop. **16**: 561–564. *t. 18.* 1772; Radlkofer in Engler, Pflanzenr. **IV. 165**: 1329. 1933. TYPE SPECIES: *K. paniculata* Laxm.

Sapindus L. *sensu* Murray, Linn. Syst. Veg. (ed. 13.) 315. 1774. Includes *S. chinensis* Murray (*nomen illegit.*), a substitute name for *K. paniculata* Laxm.

Deciduous trees, single or sometimes multitrunked, with gray to brown, thick, sometimes fissured bark; twigs, young branches, and petioles often prominently lenticellate; pith whitish to light brown; axillary bud scales (prophylls) 2, glabrous without, strongly sericeous within. Leaves alternate, exstipulate, imparipinnate, sometimes pinnatisect, the petioles pul-

[3] The localities, pinpointed on dot maps (FIGURES 11, 14, 16), are in accordance with standard gazetteers and atlases, as follows. **China:** *Mainland China, Gazetteer No. 22.* ed. 2. Vols. 1 & 2. Prepared by the Geographic Names Division, Army Map Service, Washington, D. C. 1968; *The Times Atlas of the World.* Vol. 1. The Times Publishing Co. Ltd., London. 1958. **Taiwan:** *Republic of China, Official Standard Names Gazetteer.* United States Board on Geographic Names, Defense Mapping Agency Topographic Center, Washington, D. C. 1974. **Fiji:** *Fiji, Tonga, and Nauru, Official Standard Names Gazetteer.* United States Board on Geographic Names, Defense Mapping Agency Topographic Center, Washington, D. C. 1974.

Herbarium acronyms are in accordance with those of Holmgren and Keuken (1974). The abbreviation KFI (Korea Forest Institute) is the only symbol not cited by Holmgren and Keuken. Where possible, coordinates have been added in brackets to pinpoint localities.

[4] Orthographic variants are *Kölreutera*, *Kolreuteria*, and *Koelreutera*, all occurring after 1772.

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detail and colpus edge, × 5900; 4, *K. bipinnata*, polar view, × 1976; 5, *K. bipinnata*, enlargement of surface detail, edge of colpus at lower left, × 5900; 6, *K. elegans* subsp. *elegans* (Fiji), polar view, × 2183; 7, *K. elegans* subsp. *elegans*, enlargement of surface detail, colpus at left, × 5900.

vinate at base, the rachis canaliculate or flattened on upper side, glabrous or densely short-hairy on the middle portion, terete beneath; leaflets usually alternate, sometimes opposite, elliptic to ovate, flat, usually more or less oblique, entire or serrate to crenate, sometimes pinnatisect to lobed, sessile or short-petiolulate, sometimes decurrent on the rachis, thick membranous to subcoriaceous, dull or sometimes lustrous, glabrous to sparsely

FIGURE 8. *Koelreuteria paniculata* (*Meyer 12570*, cultivated): habit and mature capsules, × ¼.

pubescent, sometimes glandular on the veins, mainly beneath, the median leaflets usually largest. Inflorescence terminal, paniculate, pyramidal, loosely branched; flowers polygamous, both the staminate and carpellate on the ultimate tertiary or quaternary branchlets, bracteate, acropetal, racemose, manifestly regular at first, becoming asymmetric, pedicellate; calyx lobes 5, 3 long and 2 short, valvate, ovate, ciliate-glandular or puberulent, often persistent; disc slightly oblique, lobulate, on a short androgynophore, more or less undulate-lobed and depressed; petals 4–5 (6), unguiculate, inserted at the base of the androgynophore, claw up to twice as long as the calyx lobes, strongly villous, limb glabrous, strongly reflexed, appendages simple to compound, folded and undulate, yellow at first, changing to orange-red at anthesis; stamens usually 8 (9), rarely fewer, on a raised, slightly oblique disc, filaments with long straight hairs mostly on the lower half, declinate at anthesis; anthers antrorse, with short straight evanescent hairs on the face and margins; pollen grains 3-colporate. Ovary on the disc, 3-locular, placentation parietal; ovules usually 6, 2 in each locule, more or less median, anatropous, 3 descending and the raphe dorsal, 3 ascending and the raphe ventral; style exserted, stigmas 3. Capsules triangular in cross-section, connate near base, inflated in upper portion, conoidal or ellipsoidal, sparsely hairy at first, becoming glabrous, loculicidal, the valves winglike, papyraceous, reticulate-veined, ovate and tapered or rotund to suborbicular. Seeds subspherical to pyriform, black or brown, shiny, sometimes partially or entirely covered with a whitish waxlike coating, bony, with an exalbuminous, spirally convolute embryo, the funiculus persistent, forming a short stipe; seedlings epigeal, with narrow, strap-shaped cotyledons; base chromosome number 11.

VERNACULAR NAMES. The commonest English name for *Koelreuteria* is goldenrain-tree. The name *Luan Shu* is applied in China, although many other names are used on a regional basis (Chen, 1957): *Shih Luan Shu*, rock Luan tree (Chekiang); *Hei Yeh Shu*, black-leaf tree, and *Mu Lan Ya*, teeth of wooden railing (Honan); *Hei Se Yeh Shu*, black-leaf tree (Hopeh); *Shan Ch'a Yeh*, mountain-tea leaves (northeast region); *Yuan P'ang*, soft stick (Shantung); *Luan Hua* (from an old Chinese book on plants); *Mu Luan*, woody Luan (from a Chinese materia medica for famine relief).

KEY TO THE SPECIES

A. Leaves pinnate, rarely bipinnate; leaflets coarsely crenate-serrate to pinnatisect and lobulate, abruptly to narrowly acuminate, often apiculate; valves of capsule ovate, tapering to apex, greenish to tawny while young, dark lustrous brown when mature. China. Naturalized in Korea and Japan. . . . . 1. *K. paniculata*.

A. Leaves bipinnate; leaflets entire to shallowly serrate, tapering at tip, usually not apiculate; valves of capsule rotund to suborbicular, rose-purple while young, brown to tawny at maturity.

B. Leaflets weakly oblique, acute to short-acuminate, entire or uniformly

serrate (the lower leaflets never pinnatisect); petals 4, rarely 5; calyx lobes fimbriate-glandular; capsule with valves 3.7–6.6 cm. long, 3–5 cm. wide. Southern to southwestern China. . . . . 2. *K. bipinnata.*

B. Leaflets strongly oblique, long-acuminate to sometimes caudate, entire or irregularly crenate-serrate (the lower leaflets occasionally pinnatisect); petals commonly 5 or 4, rarely 6; calyx lobes ciliate-glandular, with short-clavate, often amber-colored to reddish glands; capsule with valves 3.4–5(–6) cm. long, (2.5–)3.1–4.6 cm. wide. Taiwan, Fiji. . 3. *K. elegans.*

1. **Koelreuteria paniculata** Laxm. in Nov. Comm. Acad. Sci. Imp. Petrop. **16**: 561–564. *t. 18.* 1772; Aiton, Hort. Kew. **2**: 7. 1789; Mirbel in Duhamel, Traité des arbres et arbustes (ed. 2) **1**: 165. *t. 36.* 1801; Martyn, Miller Gard. Bot. Dict. (ed. 9) **2**: *n. 1.* 1807; Rees, Cyclop. **20**: I. pt. 39. 1812; Bunge in Mem. Div. Sav. Acad. Sci. St. Petersburg **2**: 85. 1835; Sieb. & Zucc. in Abh. Bayer. Acad. **4**(2): 153. 1845; Forbes & Hemsley in Jour. Linn. Soc. Bot. **23**: 138. 1886; Elwes & Henry, Trees Gr. Brit. & Ireland **7**: 1932, 1933. 1913; Radlk. in Engler, Pflanzenr. **IV. 165**: 1330. 1933; How & Ho in Acta Phytotax. Sinica **3**: 405. 1955. LECTOTYPE: *Laxmann s.n.* (LINN, No. 514.5; ICC Micro. ed. hb. LINN, card 268). FIGURES 1–3, 8, 9, 11.

Sapindus chinensis Murray, Linn. Syst. Veg. (ed. 13) 315. 1774; Linn. f. Suppl. Pl. (ed. 2) 228. 1781; Murray, *Ibid.* (ed. 14) 380. 1784; Murray, *Ibid.* (ed. 15) emend. Persoon, 407. 1797; Murray, *Ibid.* (ed. 15) 311. 1798; Poiret in Lamarck, Encycl. Méth. Bot. **6**(2): 667. 1805 (*nomen illegit.*). A substitute name for *K. paniculata* Laxm.

Sapindus sinensis J. F. Gmelin, Linn. Syst. Nat. (ed. 13) **2**: 642. 1791; Linn. Syst. Veg. **1**: 642. 1796, reprinted from ed. 13. 1791 (an orthographic variant based on *Sapindus chinensis* Murray).

Koelreuteria chinensis (Murray) Hoffmannsegg, Verzeich. Pflanzenkult. 70. 1824, *pro syn.*

Koelreuteria paullinioides L'Hérit. Sert. Angl. 11. 1789; *Ibid. pl. 19.* 1792, mislabeled *K. paniculata.* Type specimen not seen.

Koelreuteria japonica Hassk. Cat. Hort. Bog. Alt. 226. 1844, *nomen nudum.*

Koelreuteria paniculata β var. *japonica* Siebold in Jaarb. Kon. Nederld. Maatsch, Aanmoed. Tuinbouw. 31. 1844, *pro syn.*

Koelreuteria apiculata Rehder & Wilson in Sarg. Pl. Wilson. **2**: 191. 1914; Chung in Mem. Sci. Soc. China **1**: 152. 1924; Radlk. in Engler, Pflanzenr. **IV. 165**: 1333. 1933; Rehder, Man. 584. 1934; Lee, For. Bot. China 789. 1935. LECTOTYPE: *Wilson 2370b* (A); isolectotype (US), fruit. Collected September, 1908. It is necessary to select a lectotype specimen to separate flowering and fruiting specimens, collected on different dates and originally assigned the same field number, *Wilson 2370.*

Koelreuteria paniculata var. *apiculata* (Rehder & Wilson) Rehder in Jour. Arnold Arb. **20**: 418. 1939; Chun in Sunyatsenia **4**: 239. 1940; Rehder, Man. (ed. 2) 592. 1940; *Ibid.* Bibl. 434. 1949.

Koelreuteria bipinnata Franchet var. *apiculata* (Rehder & Wilson) How & Ho in Acta Phytotax. Sinica **3**: 407. 1955. Based on *Wilson 2370* = *K. paniculata* Laxm.

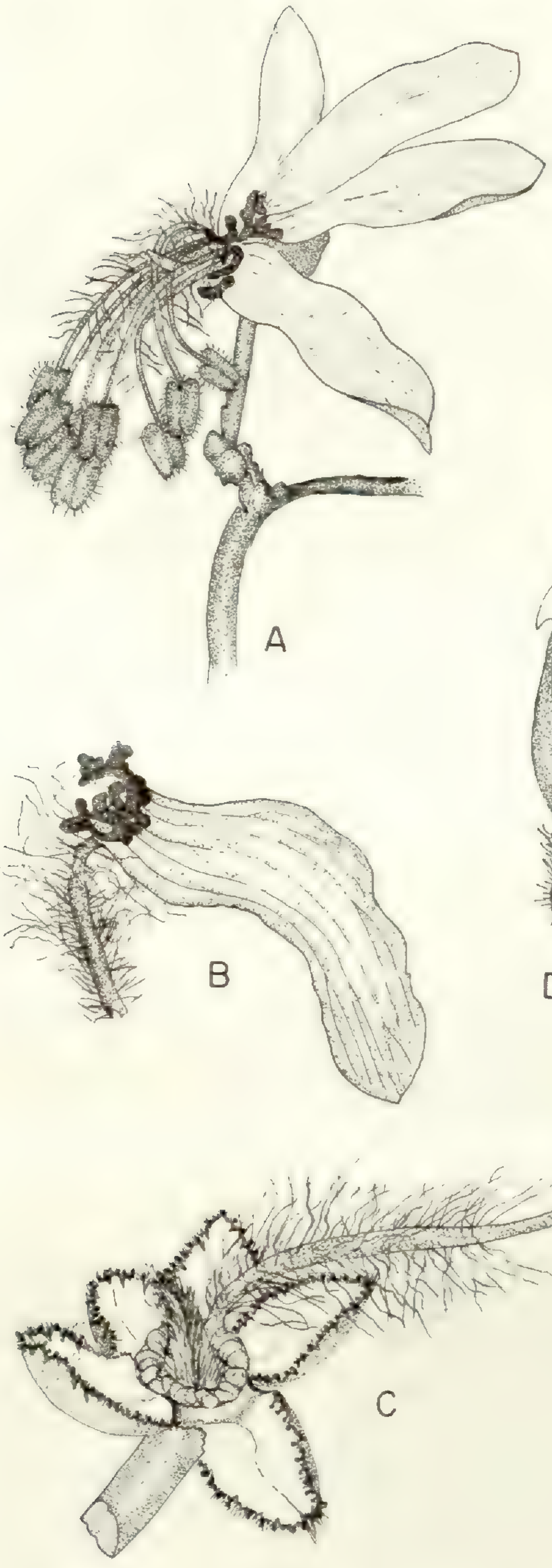

FIGURE 9. *Koelreuteria paniculata*: A, staminate flower, × 6; B, corolla lobe, showing villous claw and limb with basal appendages, × 12; C, staminate flower, showing erose-glandular calyx lobes, raised disc, abortive ovary, and stamen with antrorse anther immediately before anthesis, × 6; D, young capsule shortly after anthesis, torn open to show position of seeds, one descending and the raphe dorsal, in the adjacent valve ascending and the raphe ventral, × 6; E, stamen, ventral view, setulose on antrorse face and on margins on dorsal side; filaments villous in lower portion, × 14; F, stamen, dorsal view, setulose only on the margins, × 14.

Tree to ca. 13 m. in height and to ca. 50 cm. in diameter; bark thick, gray-black, longitudinally furrowed; lenticels gray to dark brown, small, not very prominent; twigs glabrous or sometimes puberulent below the inflorescence. Leaves spreading, pinnate or rarely bipinnate, 25–50 cm. long, 10–25 cm. wide; rachis usually glabrous on lower side, with scattered hairs on upper side; leaflets 11–18, cuneate to truncate, only barely unequal at base, narrowly to broadly ovate to elliptic, 4.8–10.7 cm. long, 2.8–6.9 cm. wide, coarsely crenate-serrate to pinnatisect and lobulate, abruptly to narrowly acuminate, often apiculate at tip, veins faint above, slightly raised beneath, usually with scattered very short crispate hairs on the midvein above, the hairs beneath longer and in tufts along the midvein, sometimes mixed with scattered glands, margins sometimes ciliate; petiolules very short, 1–2 mm. long, often densely hairy. Inflorescence 25–30 cm. long, as much across, densely puberulent, especially on the ultimate branchlets, and with scattered glands. Flowers slightly fragrant; pedicels 2.5–5 mm. long; calyx lobes erose-glandular on margin, glabrous on back or glandular-hairy; petals 4, limb 4.5–7 mm. long, 1.5–2 mm. wide, acute, primrose yellow (*4A*, Royal Horticultural Society Colour Chart, London, 1966), appendages with few folds, primrose yellow at first, changing to orange-red (*34A*, *Ibid.*) at anthesis, claw 1–2.5 mm. long, densely villous with ascending hairs, and partly orange-red; stamens long-exserted, filaments densely villous with spreading straight hairs, especially in the lower half and at base, anthers lavender. Capsules conoidal, the valves ovate (placenta protruding as a winglike projection from each valve), tapering to apex, apiculate, 4.3–6.9 cm. long, 2.5–3.2 cm. wide, greenish to tawny while young, dark lustrous brown at maturity, reticulate-veined on the outside, smooth and somewhat lustrous on the inside; styles 3–5 mm. long; seeds nearly spherical, 6–7 mm. × 6.5–8 mm., black; $2n = 22$.

DISTRIBUTION. China, from Liaoning Province in the northeast, southwestward through the central provinces to Yunnan; also cultivated in gardens. Although reported by Chun (1940) from Kweichow and Kwangsi, the specimens actually represent *Koelreuteria bipinnata*.

Flowering mid-June to mid-August; fruiting August and September. Mature capsules with seeds may persist on the tree well into winter and even to the next flowering season. Various habitats have been recorded: river courses, open forest areas, rocky mountain slopes, and valleys mainly in well-drained soils from near sea level to 300 m.

REPRESENTATIVE SPECIMENS. **China.** ANHWEI: Chuchow [33.19N, 118.18E], *Tsu 529* (UC). CHEKIANG: locality undesignated, *Barchet s.n.* (MO). HONAN: near Hou-tien [33.18N, 112.28E], 2500 ft., *F. N. Meyer 1855* (NA); Im Kreise Teng fong, 530 m. [34.27N, 113.02E], *Schindler 131* (A, BM, E, G, K, W). HOPEH: Tientsin [39.08N, 117.12E], *Clemens s.n.* (E); Changli [39.44N, 119.13E], *Clemens 6237* (E); Hsiaowutaishan [39.57N, 114.59E], *Fan Memorial Institute 61773* (A); Men-Tau-Kou [39.56N, 116.02E], *T. F. King 175* (NY, S); Paita, *Licent 9652* (W); Tschili, Duang hu dien, *Limpricht 2969*

(K, S); western tombs, 200 m., *Liu 478* (A, K); Jehol (Chengteh) [40.48N, 118.06E], *Nakai, Honda, & Kitagawa s.n.* (TI); Hsiang Shan, *Sheehan 239* (NY). HUPEH: Huan-tou-san [31.15N, 114.15E], *Hugh s.n.* (BM). KANSU: Lanchou [36.03N, 103.41E], *Piasetski s.n.* (LE); eastern Kansu, anno 1885, *Potanin s.n.* (LE); Pai-shuiho, Kuangting, *Potanin s.n.* (LE); banks of Chulungapu-Nyipa, lower Tebbu country [34.23N, 103.01E], *Rock 14994* (A); dry slopes of Nyi-baku, lower Tebbu country, 7500 ft. [34.23N, 103.01E], *Rock 14796* (A, E, K, P, UC, W); Peshwekian gorge, lower Tebbu country, 6800 ft. [32.48N, 105.07E], *Rock 14553* (A, C, LE, S, US). KIANGSU: near Nanking, *Carles 557* (E, K); Paohwashan, *Cheng 4500* (P); Chuyong, *Ling 2179* (UC); Ming tombs near Nanking, *F. N. Meyer 1450* (A, NA); Hwang San Yü, *Ren & Tao* (UC); Mao Shan, Tan Yang [32.0N, 119.35E], *Tso 1793, 1814* (A). LIAONING: Manchuria, Fu-shun (Shen-yang) [41.50N, 123.26E], *Yamatsuta 1006* (TNS). PEKING MUNICIPALITY: envir. Pekin, anno 1831, *Bunge s.n.* (K, LE, P); mts. west of Peking, *Bretschneider s.n.* (A, BM); rocky hillside north of summer palace, *Dorsett & Morse 5585* (A, NY, P, US); Prince Park, Peking, *Liuo 7119* (K); on city wall, Peking, *F. N. Meyer 1013* (A, MBG, NA, NY, P, TI). SHANSI: Mien Shan [36.49N, 112.02E], *Chaney 1041* (NY, UC); Hwo shan (mts.) [36.40N, 112.05E], *Kabanov s.n.* (LE); east of Changchiagou, Wenshui [37.25N, 112.01E], *Kang 150* (GH); Tchangkiatchoang, Tchely S.E., *Licent 82* (P); Tsinn choei s'hien [36.45N, 112.41E], *Licent 1464* (BM, P); Chin Yuan, near Hsu Chio-Chuan [36.29N, 112.20E], *Ling 1621* (A, UC, US); Shueiyu [39.14N, 113.14E], *Sandberg 163* (S); Hsia-hsien, Pei-shui-ko and Yüan-ch'ü Dist., Ssü-chiao-ho, 900 m. [35.05N, 111.24E], *H. Smith 6103* (A, S). SHANTUNG: Meng Shan, Fei Hsien [35.16N, 117.57E], *Cheo & Yen 246* (A, BM, G, P, W); Tsinanfu-Lung Tung, 300 m., *Chiao 3086* (A, B, C, E, G, K, LE, NY, UC, US); Po-shan [36.29N, 117.50E], *Kao 529* (A); Fangtse (Weihien), *Royal Forest Station 328* (B). SHENSI: Tsinling-shan, Nauwutai pr. Hsingan [32.42N, 109.12E], 1500–1700 m., *Fenzel 68* (W); Tsinling-shan centr. inter Mei et Liupa [33.40N, 106.55E], *Fenzel 658* (W); Ningshenhsien, 1150 m., *Kung 3073* (PE). SZECHUAN: Wei Kuan [31.29N, 103.16E], *Bock & Rosthorn 2523* (A); near Hua Nin Pink, Han Yuen Hsien [29.21N, 102.43E], 2100 m., *Chiao 1876* (A); Litang valley, Muli Dist. [28.20N, 100.48E], 10000–11000 ft. alt., *Forrest 21330* (A, E, K, P, W, US); supra vicum Helugö in convalle fluminis Yalung ad septentriones oppidi Yen-yüen infra castellum Kwapi [27.30N, 101.40E], 2325 m., *Handel-Mazzetti 2467* (A, W); River Valley of Fu pien [31.18N, 102.27E], *Potanin s.n.* (LE); near Tachienlu (Ta-tsien-lou) [30.03N, 102.02E], *Pratt 138* (BM, DUB, E, G, GH, K, LE, P, US); mts. between Litang & Shou-Chu rivers, 3180 m., *Rock 16904* (A, E, NY, US, W); Fu-pien Hsien [31.18N, 102.27E], 2750 m., *C. Wang 21321* (A, TAI); Li-fan Hsien [31.32N, 103.19E], 3000 m., *C. Wang 21608* (A); Mon-kong Ting, *E. H. Wilson 278* (A, NA, photos); Fei-yueh-ling, near Tung River, *E. H. Wilson 277* (A, NA, photos); northeast of Tachien-lu, dry valleys near Romichango, *E. H. Wilson 2370* (A, US; *2370a* lectotype of *K. apiculata*). YUNNAN: Yen Ching Shan [25.54N, 98.58E], *Forrest 30068* (E); Muli, Kehsy [23.59N, 105.22E], *Yü 14214* (A, E); Muli, near Lamasery, *Yü 14860* (A, E). PROVINCE UNDESIGNATED: N. central China, Mt. Miao-uan-san, *Hugh s.n.* (BM); N. central China, Mt. Theu-kio-tsuen, *Hugh s.n.* (BM); N. central China, Mt. Lao-y-san, *Hugh s.n.* (BM); Kyoyokuwan-Sanho, *Togashi 741* (TNS). **Japan** (naturalized). HONSHU. AOMORI PREF.: Hirosaki, *Knashi 453* (KYO); FUKUI PREF.: Prov. Echizen, Ayukaya, Kunimimura, Nyu-gun, *Tashiro s.n.* (TNS); Wada Takahama-cho, Ooi-gun, *Kuwashima 15037* (TNS); Iwayama-hill, Takahama-cho,

Prov. Wakasa, *Hori s.n.* (KYO); Takahama, Prov. Wakasa, *T. Nakai 1052* (KYO); Shiroyama in Takahama-cho, Prov. Wakasa, Ikenokochi, Togo-mura, Tsuruga-gun, *Tashiro s.n.* (KYO). HYOGO PREF.: Kasumi-cho, Kinosaki-gun, *J. Araki s.n.* (KYO); Kasumi-cho, Kinosaki-gun, *Hosomi s.n.* (KYO). ISHIKAWA PREF.: Ayukawa, Kunimi-mura, Niu-gun, *Tashiro s.n.* (KYO); Prov. Noto, Togi, *Kitamura s.n.* (KYO). IWATE PREF.: côtes de Kessenuma, *Faurie 6082* (G, P); Tsubaki-jima, Shizugawa-wan, Prov. Rikuzen, *Suzuki s.n.* (TNS). MIYAGI PREF.: Prov. Rikuzen, Motoyoshigun, Iwaisaki, *Sohma & Ohashi 127* (TI). NAGANO PREF.: Prov. Shinano, Mt. Hiuchi, *Sakurai s.n.* (A). **Korea** (naturalized). Anmyun-Do, Choong-Nam [36.30N, 126.22E], *Cho s.n.* (KFI); Ouen san [38.21N, 127.55E], *Faurie 64* (A, BM, KYO, LE, P, W); Deukjog Island [37.15N, 126.35E], *T. B. Lee s.n.* (SNU); Daebu Island [37.15N, 126.35E], *T. B. Lee s.n.* (SNU); Riverside, Suwon [37.16N, 127.01E], *Lee, Park, & Cho 3251* (SNU); Anmin Island, *Lee & Cho s.n.* (SNU); Sorai Beach, Whanghai Prov., *Mrs. R. K. Smith s.n.* (A, US); Koko, Prov. North Kesho [36.05N, 129.22E], *E. H. Wilson 8487* (A).

CULTIVATED. **Africa: Tunisia.** Jardin Mopitant, *Cuenod s.n.* (G). **Asia: China.** Summer palace grounds, Peking, *Armacost 95* (NY); Peking-Seityokuon Engeisikenzyo, *Togashi 2418* (TNS). **Hong Kong.** Hort. *Bot. & Forestry Dept. 5923* (K). **India.** New Forest, Dehra Dun, *Raizada 2080* (E); Mangalor, Terr. Canara, *Hohenacker s.n.* (P). **Israel.** Jerusalem, *Linder s.n.* (S). **Japan.** Hirosaki, Aomori Pref., *Faurie 3452* (KYO, P); Tokyo, *Goto s.n.* (TAI); Prov. Chikuzen, Rukuoka Pref., Tokko Temple, Kyushu, *Kanisi s.n.* (TAI); Prov. Yamoto, Matsuyama-cho, Uda-gun, *Koidzumi s.n.* (KYO); Morinoyakuen, Uda-gun, Nara Pref., *Koidzumi s.n.* (KYO); Asakawa, Prov. Musashi, Tokyo Pref., *Kunosato s.n.* (TAI); Yokohama, 28–VII–1862, *Maximowicz s.n.* (LE); temple Matsumoto-Toko-ji, *Nikai, s.n.* (TNS); Tanigawa, Prov. Kodzuki, Pref. Gumma, *Ouoma s.n.* (NA, S); ad ripam fluvii Matsia Gawa prope pagum Saija, *Pierot 569* (L, P); Hida, Honshu, *Shio 7215* (A); Omura, Prov. Hizen, Kyushu, *Tashiro s.n.* (KYO); Prov. Sagami, Todzuka, *Togashi s.n.* (TNS); Oohara, Kyoto, *Tuyama s.n.* (TNS); Yokohama Nursery Co. (E). **Korea.** Botanical garden, Ewaha Woman's University, *T. B. Lee s.n.* (SEU). **Lebanon.** Cam Liman, Hebeli, *Post s.n.* (G). **Turkey.** Boulevard facing Jardin Municipal, Constantinople, *Aznavour 527* (G); Göksu-Tal prope viam, *Wimmer 25* (W). **U.S.S.R.** Aschabad [37.30N, 57.30E], *Bornmüller 511* (K, P, W). **Australia.** Ross Street, O'Conner, Canberra, *Darbyshire 580* (K). **Europe: Austria.** Chemischen Institut in der Währingerstrasse, *Zerny s.n.* (W); Schönbrun (W); Hort. Bot. Vind., 27 June 1806, *hb. Mertens* (LE); Landeskreuanstalt "am Steinhof," *Korb s.n.* (W). **Belgium.** Bot. Have, Bruxelles, *Lange s.n.* (C). **Bulgaria.** Deoushlea, *Petersen s.n.* (C). **Cyprus.** Dept. of Agriculture, Nicosia, *Lyenzamides 1308* (K). **Czechoslovakia.** Silesia, Opp. Opava in horto pagi Novy Dvur, *Elblova s.n.* (A); Moravia, Brünn, *Müller s.n.* (G, NY, S). **England.** Hort. Bot. Cambridge (A); Beaufort (Sussex), *Elwes* (DBN); between Gloucester Road and Earls Court, London, *Gerrans s.n.* (BM); Hampshire, *Horder s.n.* (E); Hort. Kew, *Aiton s.n.* (G); Chelsea Physic Garden, *F. G. Meyer 13962* (NA); Bromley, Kent, anno 1780, *Norman s.n.* (BM); Wakehurst Place, Ardingly, Sussex, *Wakehurst 629* (K); Cherkley Court, Surrey. *Jackson s.n.* (BM). **France.** So. France, *Ellis s.n.* (A); Arnas (Rhone), *Gandoger 333* (LE, MO); locality undesignated, anno 1786, *Lamarck s.n.* (P–LA; NA, photo); Hort. Cels, *L'Héritier s.n.* (G–DC); Arboretum segrezianum, Siene-et-Oise, Segrez, *Nicholson s.n.* (E, K); Hort. Vilmorin, Verrieres, *Vilmorin s.n.* (A); Hort. Montpellier, anno 1807 (LE); Hort. Paris, anno 1792, *Ventenat s.n.* (P–JU;

NA, photo); Jardin des Plantes, Paris, anno 1813. 1901, 1904, 1925 (P); Hort. Bot. Strasbourg, *Schneider s.n.* (A). **Germany.** Breslau, Königl. Bot. Gart., *Baenitz 1399* (A, DBN, E, GH, L, PH, S, WAG); Hort. Saltz-wedel, Frankfurt a/m, anno 1826, *Engelmann s.n.* (MO); Hort. Bot. Berol., anno 1906, *Hülphers s.n.* (S); Hort. Bot. Erlangensis, *Kaulfuss s.n.* (A); Hort. Bot. Stuttgart, *Mohr s.n.* (US); in gardens, Zweibrucken, *Mohr s.n.* (US); Darmstadt, *Purpus s.n.* (A); Schloss Heidelberg, *Springer s.n.* (WAG); George-born bij Schlangebeck, *Suringar s.n.* (WAG). **Greece.** Peloponnesus, Achaia, prope pagum "Kalavryta," *Bornmüller 349* (A, S). **Ireland.** Birr Castle, Co. Offaly, *Earl of Rosse s.n.* (NA); Donard House, Mrs. Heighington's Garden (DBN). **Italy.** Villa Taranto, Pallanza, *McEacharn s.n.* (BM); Hort. Bot. Florence, anno 1814 (S). **Netherlands.** Hort. Bot. Amsterdam, *Springer s.n.* (WAG); Bot. Gard. Cantonspark, *Mennega s.n.* (E); town garden, Haarlem, *Springer s.n.* (WAG); Helsdorf, park Graf von Spee, *Suringar s.n.* (WAG); Rengerspark, Leeuwarden, *Hoogland 434* (L); Leiden, Gemeentekwekerij, *Hattum s.n.* (L); arboretum 'De Dreijen,' Wageningen, *Bruijn 2142, 2143, 2159, 2160, 2166* (NA). **Portugal.** Jardim do Ultramar, Lisboa, *Reis s.n.* (K). **Spain.** Gerone, Figueras, *Augustin 5113* (G, W); Hort. Bot. Valencia, anno 1852, *Bourgeau s.n.* (P). **Turkey.** Birge garden Rumel Hissar, *Post s.n.* (G). **U.S.S.R.** Tbilisi, anno 1894, *O. A. & B. A. Fedtschenko s.n.* (LE); Hort. Bot. Petrop., anno 1771, *Laxmann s.n.* (LINN, lectotype; photo at NA); Hort. Bot. Nikita, Yalta, anno 1837, *Trautvetter s.n.* (LE). **North America: U.S.A.** ARKANSAS: Hot Springs, *Everett s.n.* (MO). CALIFORNIA: Willits, Mendocino Co., *Bacigalupi 9115* (UC); Lakeport, *Bonar s.n.* (A, UC); lower Orpet Park, Santa Barbara, *Broder 1246* (NA); Jackson, Amador Co., *Clemens s.n.* (CAS); Elysian Park, Los Angeles, *Hall 7992* (UC); Univ. California campus, Davis, *Hansen s.n.* (UC); Los Angeles State & Co. Arboretum, *Jativa 2269* (NA); Univ. California Bot. Gard., Berkeley, *Kruckeberg s.n.* (NY); capitol grounds, Sacramento, *McClintock & Leiser s.n.* (CAS); garden Merritt Island, 3.5 mi. so. Clarksburg, Yolo Co., *Quick 6818* (CAS); U. S. Exp. Stat., Chico, *Rixford s.n.* (CAS); Santa Clara, *Robinson s.n.* (UC); Dorothy Twisselmann Ranch, e. San Luis Obispo Co., *Twisselmann 13704* (CAS); San Bernardino, *H. A. Walker 3900* (US); Golden Gate Park, *Walther s.n.* (CAS); C. Menzies' place, Mill Valley, *Walther 81* (A, CAS); Huntington Bot. Gard., *Walther 104* (A); Bel-air, Beverly Hills, *Walther 43* (CAS). CONNECTICUT: New Haven, *Eaton s.n.* (GH). DELAWARE: Wm. P. Bancroft's garden near Wilmington, anno 1878, *Canby s.n.* (NY); Mt. Cuba Bot. Park, Greenville, *Kelsey 145* (A, K, NA); Rehoboth Ave., Rehoboth Beach, *McVaugh 6592* (GH, NA, NY). DISTRICT OF COLUMBIA: Capitol Grounds, *Lyon s.n.* (CAS); grounds, Department of Agriculture, *Sudworth s.n.* (US); Monument Grounds, *Van Eseltine s.n.* (NA); St. Elizabeth Hospital Grounds, *E. H. Walker 751* (NA); U. S. National Arboretum, *P. I. 21973* (NA), *P. I. 130117* (CAS, NA, UC). GEORGIA: so. side Coop. Ext. Bldg., Univ. Georgia, Athens, Clarke Co., *Meyer & Mazzeo 14415* (NA). INDIANA: roadside 3 mi. so. New Harmony, Posey Co., *Hermann 6132½* (NA); Sigma Nu lawn, Greencastle, Putnam Co., *Welch 6906* (GH, MO). KANSAS: Emporia, *Agrelius s.n.* (MO). KENTUCKY: Calvert City, Marshall Co., *Eggleston 4842* (NY). LOUISIANA: Hodges Gardens, Many, Sabine Parish, *Meyer & Mazzeo 11797* (NA). MARYLAND: Corner East-West Highway and Jones Mill Rd., Bethesda, Montgomery Co., *F. G. Meyer 12570* (NA). MASSACHUSETTS: Arnold Arboretum, Jamaica Plain, *21980–A* (A, C, CAS, K, MO, NA); Manning Garden, North Salem, *Morse s.n.* (A); Hort. Brookline, *Sargent s.n.* (A); President Clark's place, Amherst, *Stevens s.n.* (US); Rockport, *Wagenknecht & Howard s.n.* (A). MISSISSIPPI:

"Mistletoe," garden of S. H. Lambdin, Natchez, Adams Co., *Meyer & Mazzeo 11688* (NA). MISSOURI: Kansas City, *Bushnell s.n.* (GH); Tower Grove Park, St. Louis, *Croat 8830, 8877* (MO); Univ. Missouri campus, *Drushel 1983* (P); Missouri Botanical Garden, *Kellogg s.n.* (CAS); Webster Groves, *Lodewyks s.n.* (MO). NEVADA: grounds of Lahonton Motel, Fernley, Lyon Co., *Follett s.n.* (CAS). NORTH CAROLINA: Biltmore, Buncombe Co., *Biltmore 9624* (G, P, S, UC, W); Winston-Salem, *Schallert s.n.* (W). NEW JERSEY: institute grounds, Freehold, *Wood s.n.* (NY); Duke's Park, Somerville, *Fisher s.n.* (PH); New Egypt, *Grove 804* (PH). NEW MEXICO: college farm, Mesilla Park, *Standley s.n.* (US). NEW YORK: Ithaca, *Bailey 602* (NA); University Heights, New York Univ. campus, *Drushel 1923, 2838* (P); Riverside Park, New York City, *Archer s.n.* (GH); New York Bot. Gard., *P. Wilson s.n.* (NY). OHIO: Ohio State Univ. campus, *Cooke s.n.* (A). OKLAHOMA: locality undesignated, *Featherly s.n.* (MO). PENNSYLVANIA: Longwood Gardens arboretum, *Bates 71* (A, NA); Happel Garden, Monocacy, Berks Co., *Brumbach 6330* (A, NA); trial plots at Fordhook Farm, Doylestown, *Dudley s.n.* (A); Barnes Arboretum, Merion, *Fogg s.n.* (CAS); Bartram's garden, Philadelphia, *Short s.n.* (MO). TENNESSEE: Agr. campus, Univ. Tennessee, *Meyer & Mazzeo 12842* (NA); garden of Sam Caldwell, Nashville, Davidson Co., *Meyer & Mazzeo 13161* (NA); Tennessee Valley Nursery, Winchester, Franklin Co., *Meyer & Mazzeo 13082* (NA). UTAH: Brigham Young Univ. campus, Provo, Utah Co., *Daines s.n.* (A); Salt Lake City, *Lindsay s.n.* (A). VIRGINIA: Maymont Park, Richmond, *Meyer & Mazzeo 14517* (NA). WASHINGTON: Seattle, *Schallert 489* (MO). **Oceania: New Zealand.** Linwood Nursery, Christchurch, *Sykes s.n.* (NA).

Both the genus and the type species, *Koelreuteria paniculata*, were based on a cultivated plant without a type specimen being designated. In the absence of a type, the plate, published with the protologue, would serve adequately as the nomenclatural type, except for the fact that a specimen does exist in the Linnean Herbarium in London. In 1771 Laxmann sent a complete leaf to Linnaeus, most likely from the type tree, along with a description of the tree, which he described in 1772 as *Koelreuteria*. The sheet in the Linnean Herbarium, furthermore, bears an annotation by Linnaeus: "Chinensis arbuscula ex Horto Petropolitano Laxman." Since the identification of the material is not in question, the specimen in the Linnean Herbarium (514.5) serves as the nomenclatural type (lectotype) of *K. paniculata* Laxmann, which in turn is the type species of the genus.

The name *Koelreuteria paullinioides* of L'Héritier, dating from 1789, is clearly a substitute name for *K. paniculata*, of 1772. However, the accompanying figure, published in 1792, is something of a puzzle. The citation of both the name and plate number in the protologue, e.g. *K. paullinioides, tab. 19* (L'Héritier, 1788), seems clear enough, yet the name *K. paniculata* appears on the plate and not *K. paullinioides*. Whether this mistake was intentional or an oversight will probably never be known. The drawing in question was executed by Redouté during his visit to Kew Gardens in 1786 and was probably completed, with the name *K. paniculata* fixed to the plate, before L'Héritier had proposed the substitute name. The wrong name on the plate, more than likely, was an oversight not caught by L'Héritier before the plate went to press. Of interest in the

whole matter is a letter from L'Héritier to Dryander, dated September 1, 1788, which provides some revealing evidence for the change in name from *K. paniculata* to *K. paullinioides* (Stafleu, 1963). In his letter L'Héritier wrote that "with regard to those [names] published only in dissertations or academic memoirs, I think that one can change them without difficulty, not for the pleasure of changing, but only if one has the opportunity of giving a better one. Take for instance *Koelreuteria* . . . the trivial name seems to me to be the one which compares the genus with the nearest allied genus," in this case *Paullinia*.

Rehder and Wilson described *Koelreuteria apiculata* (1914) as being "readily distinguished by its often simply pinnate leaves, much broader less coarsely incised leaflets with less acute teeth, by its ovate or oblong-ovate, acute sepals, its smaller petals and chiefly by its sharply pointed fruit with acute or acuminate valves." However, there is nothing constant in these characters to distinguish Rehder and Wilson's plant from *K. paniculata* itself.

By some authors, *Koelreuteria paniculata* was thought to be indigenous to Korea and Japan, but no evidence exists to support this view. However, the tree has become naturalized in both areas as a result of earlier introductions from China. The plant was not listed by Nakai (1909–1911; 1915–1936) or by Trollope (1918–1920) among the indigenous trees of Korea. Both Wildemann (1903) and Matsumura (1912) believed the plant was not indigenous to Japan, and Ohwi (1965) indicated that it is "often naturalized near seashores and sometimes planted around temples." Blume (1849) was even more definite (from the Latin): "Habitat: In China, whence, on the authority of the *Encyclopedia Japonica*, it was first brought to Japan from a monastery in the Thien tai province of Tschekiang by a wandering monk, in the year 1220, and planted in the garden of a monastery in the city of Mijako [Kyoto]." Dr. Hiroo Kanai of the National Science Museum in Tokyo (pers. comm.) strongly supports the view that *K. paniculata* was introduced to Japan from China and was planted around Buddhist monasteries, perhaps in the years following the introduction of Buddhism into Japan in A.D. 552. Now *K. paniculata* is widely naturalized in various parts of Japan, particularly on the Japan seaside of Honshu.

Koelreuteria paniculata is easily distinguished from the other two species of the genus by its predominantly pinnate leaves (although bipinnate leaves may sometimes occur), by its coarsely crenate-serrate to pinnatisect and lobulate leaflets only slightly unequal at the base, and by its capsules, which are conoidal in shape.

VERNACULAR NAMES. China: *Wu-La* (Hopeh); *Luan Shu*, Luan tree; *Mu Luan*, woody Luan; *Hei Se Yeh Shu*, black leaf tree; *Wu Yeh Kao*, black leaf plaster (Hopeh); *Cha Yeh Chu* (Peking). In the United States the names goldenrain-tree, pride-of-India, China-tree, and varnish-tree have been used, although the name goldenrain-tree is the most common.

USES. Chow (1934) wrote that *Koelreuteria paniculata* is "widely cultivated around temples, palaces, gardens, and residences in Peiping. This tree is a very widespread and widely cultivated species in China, as the tombs of officials were usually surrounded by trees of this species in former times. Preferring to grow in dry, sandy plains and valleys. The wood is hard and heavy, close-grained, fine in texture, may be used for making furniture, interior finish, and for fuel, etc. A black dye may be obtained from its leaves and a yellow dye also from its yellow flowers."

Blume (1849) indicated that in China the seeds are used in religious rites in place of rose petals, for which reason this tree is considered most sacred.

According to Chen (1957), *K. paniculata* is also used for medicine, and "the leaves can be used for a blue dye. Among the seeds sold to dyers' shops are the pea-shaped black seeds which can be used as a rosary. According to the *Book of Rites*, what should be planted on the graveyard of an emperor is *sung* (pine tree), that of a feudal prince is *po* (the cedar), of a high minister is *luan* (*Koelreuteria paniculata*), of an official is *huai* (*Sophora japonica*), and a commoner is the *liu* (willow)." Other uses in China include the use of oil from the seeds as a lubricant and as a soap.

In Japan, *Koelreuteria paniculata* has only one recorded use, the seeds as religious beads, and only one currently used vernacular name, *Mokugenji* or *Mokugenzju* (fide Miquel, 1867). The name *Sendan-bano-bodai-ju*, recorded by Blume (1849), appears to be no longer in use.

GARDENS. According to Laxmann (1772), *Koelreuteria paniculata* had been grown in St. Petersburg for about 20 years prior to 1771, fixing the date of introduction at about 1750.

In England, W. Aiton (1789) recorded that *Koelreuteria paniculata* was first grown by George William Coventry, the 6th Earl, in 1763, although the record is without further documentation. One surmises that the seeds may have been obtained from Jussieu in Paris, either directly or possibly through sources at the Royal Gardens at Kew, since *K. paniculata* was, in fact, in cultivation at Kew in 1788 (LINN, coll. J. E. Smith). An even earlier specimen dates from 1780, collected by a Mr. Norman of Bromley, Kent (BM).

In France, *Koelreuteria paniculata* was cultivated probably as early as in England, since Bernard de Jussieu received seeds from D'Incarville around 1750 (D'Incarville died in 1757). The earliest documented specimen from France dates from 1786, collected by J. B. Lamarck (P–LA).

In Germany, *Koelreuteria paniculata* was grown as early as 1796 according to Willdenow (1796).

In the United States, the earliest known introduction dates from 1809 by Thomas Jefferson, who received seeds from Madame de Tessé (for details see Betts, 1944, pp. 387 & 454).

Whether Jefferson's seedling grew to maturity is unknown; however, we know that *Koelreuteria paniculata* almost certainly became established in Philadelphia after 1809, since a Col. Robert Carr of Philadelphia sent

plants to Thomas Say of New Harmony, Indiana, via New Orleans in 1832 (Mrs. Bruce English, pers. comm.)

Cultivars of Koelreuteria paniculata

1a. **Koelreuteria paniculata** Laxm. cv. Fastigiata Krüssmann, Hand. Laubgehölze. 43. 1960; Hillier's Man. Trees & Shrubs. 1972; Bean, Trees & Shrubs (ed. 8) 2: 508. 1973. Clonotype: not seen.

Koelreuteria paniculata var. *fastigiata* Bean in Kew Bull. Misc. Inf. 4: 101. 1929; Rehder, Man. (ed. 2) 592. 1940. A clonotype specimen was not cited.

Koelreuteria paniculata f. *fastigiata* (Bean) Rehder, Bibl. 434. 1949.

A tree with a narrow fastigiate habit, the branches all more or less parallel to the main trunk. Flowering not recorded.

Specimens examined. Trompenburg Arboretum, Rotterdam, Netherlands. *F. G. Meyer 6516* (NA); U. S. National Arboretum, Washington, D. C., *F. G. Meyer s.n.* (NA).

This cultivar originated as a chance seedling at the Royal Botanic Gardens, Kew, from seeds sent to a Miss Corner, of The Grove, Hammersmith, England, in April, 1888 (Bean, 1929). Bean (1973) indicates that the mother tree still survives near the Ruined Arch at Kew. The plant is rare in botanical gardens and is only occasionally offered by nurseries.

1b. **Koelreuteria paniculata** Laxm. cv. September McDaniel & March in Am. Hort. Mag. 46(2): 95, 96. 1967. Clonotype: campus of Indiana University, Bloomington, Indiana, August 27, 1970, *Meyer & Terrell 12459* (NA).

A selection of the species which flowers at the end of August and in early September in Indiana and Washington, D. C. Normally, flowering of *Koelreuteria paniculata* occurs from mid-June to early July, although a tendency for later flowering is a known manifestation of seedling variants in cultivation.

Dr. J. C. McDaniel, of the Horticulture Department at the University of Illinois at Urbana, discovered a group of three goldenrain-trees on the university campus at Bloomington, two of which were in full flower on August 25, 1958. Later one of the trees received the name cv. September, after it had been determined that the late flowering trait was normal and consistent for the parent plant. Seedlings raised from the mother plant also tend to maintain the late flowering habit.

An unnamed variant of *Koelreuteria paniculata* with white variegated leaves was collected in England in 1885 (K).

2. **Koelreuteria bipinnata** Franchet in Bull. Soc. Bot. France 33: 463, *pls. 29, 30*. 1886; Sarg. in Gard. & Forest 1: 376, 377. 1888;

FIGURE 10. *Koelreuteria bipinnata*: habit, leaves (*Delavay s.n.*, 13 Sept. 1887); capsules (*Spalding s.n.*, 29 Oct. 1971, cultivated), × ¼.

Franchet in Pl. Delavayanae 2: 143. *pls. 29, 30.* 1889; Smith in Forbes & Hemsley, Jour. Linn. Soc. Bot. 36: 487. 1904; Elwes & Henry, Trees Gr. Brit. & Ireland 7: 1931. 1913; Radlk. in Engler, Pflanzenr. IV. 165: 1332. 1933. LECTOTYPE: *Delavay 1870a* (P),

flowers. Collected July 26, 1885. It is necessary to select a lectotype specimen to separate flowering and fruiting specimens, collected on different dates and originally assigned the same number, *Delavay 1870*.
FIGURES 1, 4, 5, 10–12.

Koelreuteria integrifoliola Merr. in Philipp. Jour. Sci. **21:** 500. 1922; Radlk. in Engler, Pflanzenr. **IV. 165:** 1334. 1933. HOLOTYPE: (*McClure*) *Canton Christian College 7060* (A); isotypes (NY, UC, US).

Koelreuteria bipinnata var. *puberula* Chun in Acta Phytotax. Sinica **3:** 408. 1955. HOLOTYPE: *Ching 7668* (Herb. Biol. Lab. Sci. Soc. China, Nanking, not seen); isotypes (A (two sheets), NY, UC, US).

Tree to ca. 20 m. in height and to ca. 60 cm. in diameter; lenticels round to lens-shaped, pustulate, corky, cinnamon-brown; twigs glabrous to uniformly puberulent. Leaves spreading, bipinnate, 27–30 cm. long, 23–40 cm. wide; rachis with a line of short hairs on the upper side or glabrous; leaflets (3–)8–10(–12) on the major leaf divisions, weakly oblique, dull dark green with rather prominent impressed veins above, cuneate to rounded at base, narrowly ovate to narrowly elliptic, 7.8–14.1 cm. long, 2.1–5.1 cm. wide, entire or uniformly serrate except at base, acute to short-acuminate, the terminal leaflet sometimes narrowly obovate, as large as or larger than the others, short-puberulent on the midvein above, the hairs beneath longer and in tufts, sometimes mixed with crispate hairs and glands, rarely glabrous, sessile or with petiolules to 3 mm. long. Inflorescence 35–70 cm. long, 20–40 cm. wide, densely puberulent, sometimes glandular; pedicels 2–3 mm. long with scattered hairs; calyx lobes ovate, obtuse, to more or less deltoid and acute, fimbriate-glandular, otherwise glabrous or with scattered hairs on the outer face; petals 4 (the 5th petal often rudimentary), limb 5.5–9.5 mm. long, 1.5–3 mm. wide, obtuse or sometimes acute, appendages often deeply lobulate-undulate, claw 2–3 mm. long, up to twice as long as the calyx lobes, densely villous mainly on margins and at base; stamens long-exserted, with scattered long straight hairs, especially in the lower half, anthers gray to blackish. Capsules ellipsoidal, the valves elliptic to rotund (placenta continuous and nonwinged), 3.7–6.6 cm. long, 3–5 cm. wide, inner side somewhat lustrous, reticulate-veined on outer side, rose-purple while young, with scattered hairs on middle of valves, brownish at maturity; styles 3–4.5(–6) mm. long; seeds nearly spherical, 5.5–6 mm. × 5.5–7.5 mm., dark brown.

DISTRIBUTION. China: Anhwei, Chekiang, Hunan, Hupeh, Kiangsi, Kiangsu, Kwangsi, Kwangtung, Kweichow, Szechuan, and Yunnan; also cultivated in gardens.

Flowering ranges from July 10 to August 28 (September 30 recorded on one specimen), with fruiting from the middle of August to October. Cultivated plants usually flower in late August and September and fruit in October and November. Various habitats have been recorded: open fields, hillside forests, light woods, thickets, and roadsides, from altitudes of 250 m. to 2600 m.

REPRESENTATIVE SPECIMENS. **China.** ANHWEI: Wu Yuen [29.17N, 117.54E], *Ling 7871* (UC). CHEKIANG: Ningpo Hills, *Barchet s.n.* (US); Hangchow [30.15N, 120.10E], *Ching 2604* (A), *3768* (UC); Tien moo shan [30.15N, 120.07E], *Ching 5199* (A); Ningpo, *Faber 54* (A, K, LE, NY, P); West Lake, *Y. L. Keng 1200* (A, UC); near Linhota, Hangchow, *Migo s.n.* (A). HONAN: Chi-Kung Mt. [31.51N, 114.07E], *Li, Chang, & Ni 161* (PE). HUNAN: Ch'ien-Yang Hsien, Hsueh-Feng Mt. [27.36N, 110.50E], An-Chiang Agricultural

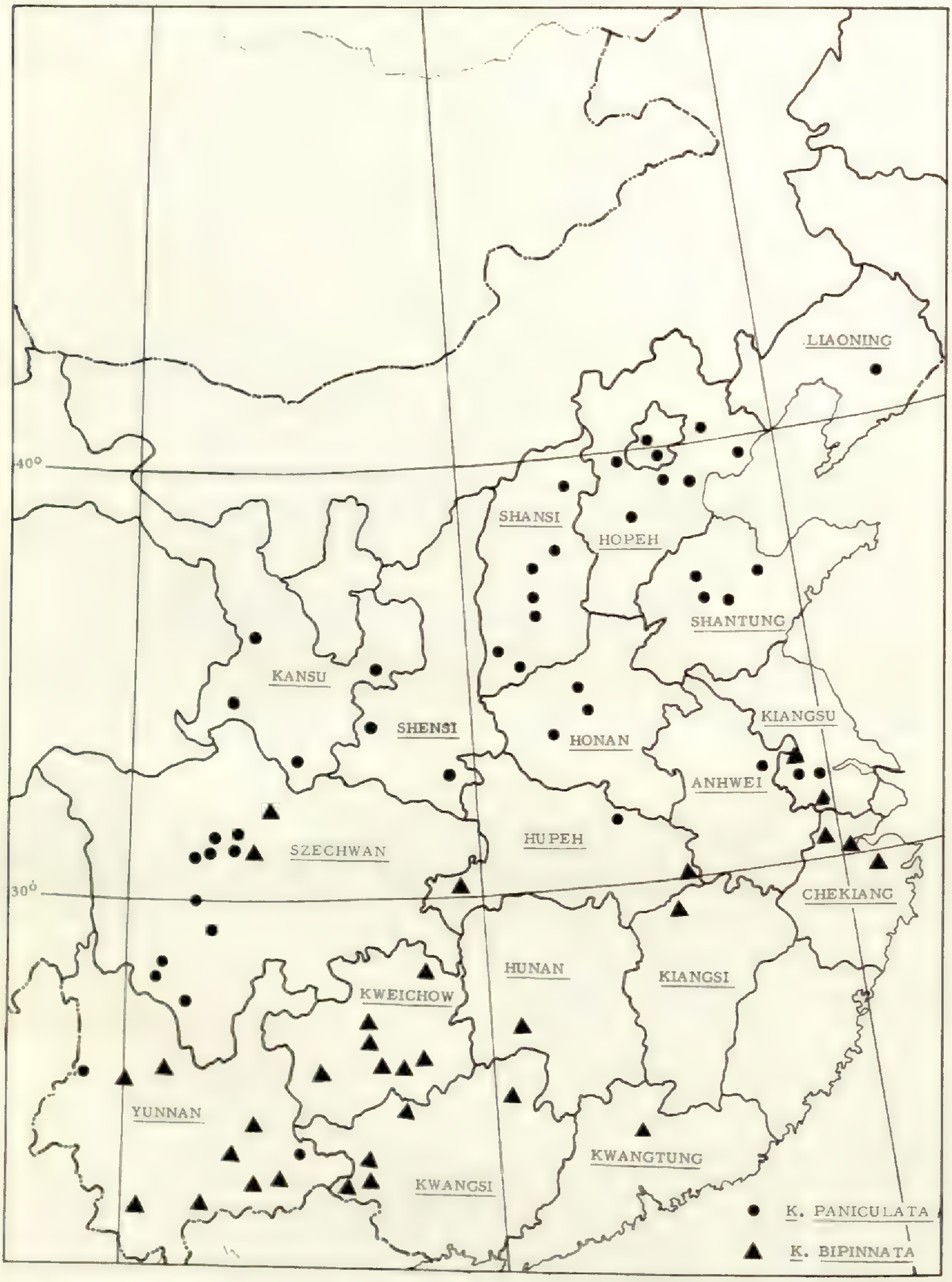

FIGURE 11. Distribution map of *Koelreuteria paniculata* (circles) and *K. bipinnata* (triangles).

School, 9 Sept. 1953 (PE); inter vicos Gauschasse et Lududsai distr. Wukan et Pautjing, *Handel-Mazzetti 12552* (A, W); Heng-Shan Hsien, Nan-Yo [27.15N, 112.44E], *0783 Hunan Team* (PE). HUPEH: Chienshih Hsien [30.37N, 109.38E], *Chow 1538* (A, E, NY); Nang Yang Ho [30.32N, 116.04E], *Chun 3865, 3868* (A), *4210* (E); W. Hupeh, *E. H. Wilson 1609* (A, DBN, E, LE, NY, P, US, W). KIANGSI: Che-yi-shuan, Kwang-kan shan Mt., *Hsiung 06409* (A). KIANGSU: Purple Mt., *Chiao 342* (UC); Kai-wei monastery, V. I-Shing, *H. Keng 2615* (A); Shan-Chien monastery, V. I-Shing [31.22N, 119.50E], *H. Keng 2536* (A). KWANGSI: Bako Shan, w. Po-Seh Hsien [23.54N, 106.37E], *Ching 7668* (A, NY, UC, US); Ching-Hsien, An-Teh village, *Ko 55806* (A); Ching Sai, rd. to Piao-Lin village [23.08N, 106.25E], *Ko 55523* (A); Ling Wun Dist., *Lau 28685* (A); Ta-chiang-yuan village & vicinity, Chin-kang-shan, Kwei-lin Dist. [25.17N, 110.17E], *Tsang 28321* (A, NA, UC, US); Nan-Tan Hsien, Wang Chang [24.58N, 107.33E], *Wang 40962* (A). KWANGTUNG: Lo-Fou Mt., Hua-Shou T'ai [23.54N, 113.54E], (*N. C. Chen*) *Academia Sinica 41678* (PE); Ying Tak Dist., Fringer Pt. Temple [24.10N, 113.24E], *Levine 3484* (A, NA); Shuikwaan, on river banks near the monastery at low altitudes, (*McClure*) *Canton Christian College 7060* (A, NY, UC, US); Yam No Mt., Mui Uen Dist., *Shang 74* (A, NA). KWEICHOW: Pin-fa [26.04N, 107.03E], *Cavalerie 197, 3190* (BISH, E, G, NA, P); Man cu Cho, *Schock 405* (A, S, US); Szenan [27.56N, 108.14E], *Steward, Chiao, & Cheo 345* (A, BM, LE, NY, P, S, W); Swan-liu, *Teng 90749* (A); Sanhoa, Yao-ren-shan [25.59N, 107.52E], 400 m., *Tsiang 6237* (A, NY), *6367* (PE, NY); Tuhshan [25.50N, 107.32E], 400 m., *Tsiang 6606* (NY, PE), *6747* (NY); Pingchow [25.50N, 107.19E], *Tsiang 7097* (NY); Kweiyang [26.35N, 106.43E], *Tsiang 8490* (NY); Siuwen [26.51N, 106.35E], *Tsiang 8701* (NY). SZECHUAN: Kuan-hsien [31.00N, 103.37E], *Chien 5368* (E, UC); Pehchuan Hsien (Síhchuan), *Fang 5566* (A, E, NA, P). YUNNAN: in silva Ta-long-tan, supra Tapin-tze, *Delavay 1870a* (P, lectotype); Ta-long-tan, 21 July 1886, *Delavay s.n.* (BM, C, E, G, P), *Ibid.*, 13 Sept. 1887, *Delavay s.n.* (BM, E, G, LE, NY, P); Lao-kouy-chan, près My-le [24.37N, 103.34E], *Ducloux 3995* (P); Wen-shan-hsien, Shii-guu [23.44N, 104.14E], *Feng 11387* (A); Si-chour-hsien, Hsin-Cheih [23.27N, 104.40E], *Feng 12611* (A); mts. to no. of Mengtsze [23.20N, 103.21E], 7000 ft., *Henry 9099* (A); Hsi-ling-ten village, 5500 ft., Mengtsze, *Henry 9103* (A, E, KE, MO, NY, S, US); Pat-ching [22.50N, 100.24E], *McLaren 215* (C, E); forêts de San-kia, 2600 m., *Maire s.n.* (P); Hay-y près Lou lan [22.54N, 102.03E], *Ngueou 673* (E); env. de Ou-se-tchong, *Sen 3025* (BM, P); Mao Nieou chan, via Pien kio ad ta pen tse [26.16N, 101.04E], *Ten 288* (A, E).

CULTIVATED. **Africa: Egypt.** Barrage Medicinal Garden, *Ibrahim & Mahdi 152* (CAI, NA); Agricultural Museum Garden, Dokki, Giza, *Mahdi s.n.* (CAI, NA); Plant Island, Assuan, *Mahdi 58* (CAI, NA); Zoological Garden, Giza, *Mahdi s.n.* (CAI, NA); Orman Garden, Giza, *Mahdi s.n.* (CAI, NA); Faculty of Agriculture, Giza, *Hadidy s.n.* (CAI, NA); Alfred Bircher's garden, El Saff, *Täckholm & Elsayed s.n.* (CAI, NA). **Asia: China.** SZECHUAN: Kiating, *Tai 295* (A). **Japan.** Government Forest Exp. Station, Asakawa, Pref. Tokyo, *Hayashi s.n.* (TNS); Kyoto, Takeda Herbal Garden, *Takahashi 286* (NA). **Europe: England.** Temperate house, Royal Botanic Gardens, Kew, *Elwes & Henry s.n.* (DBN); Arboretum, Royal Botanic Gardens, Kew, anno 1912, *Bean s.n.* (K). **Ireland.** Birr Castle, Co. Offaly, *Earl of Rosse s.n.* (NA). **North America: U.S.A.** CALIFORNIA: 1616 Gillespie Street, Santa Barbara, *Broder s.n.* (NA); Los Angeles State & County Arboretum, *Jativa 2264, 2266, 2268, 2270* (NA); residential planting, Montecito, Santa Barbara Co., *McClintock s.n.* (CAS); Univ.

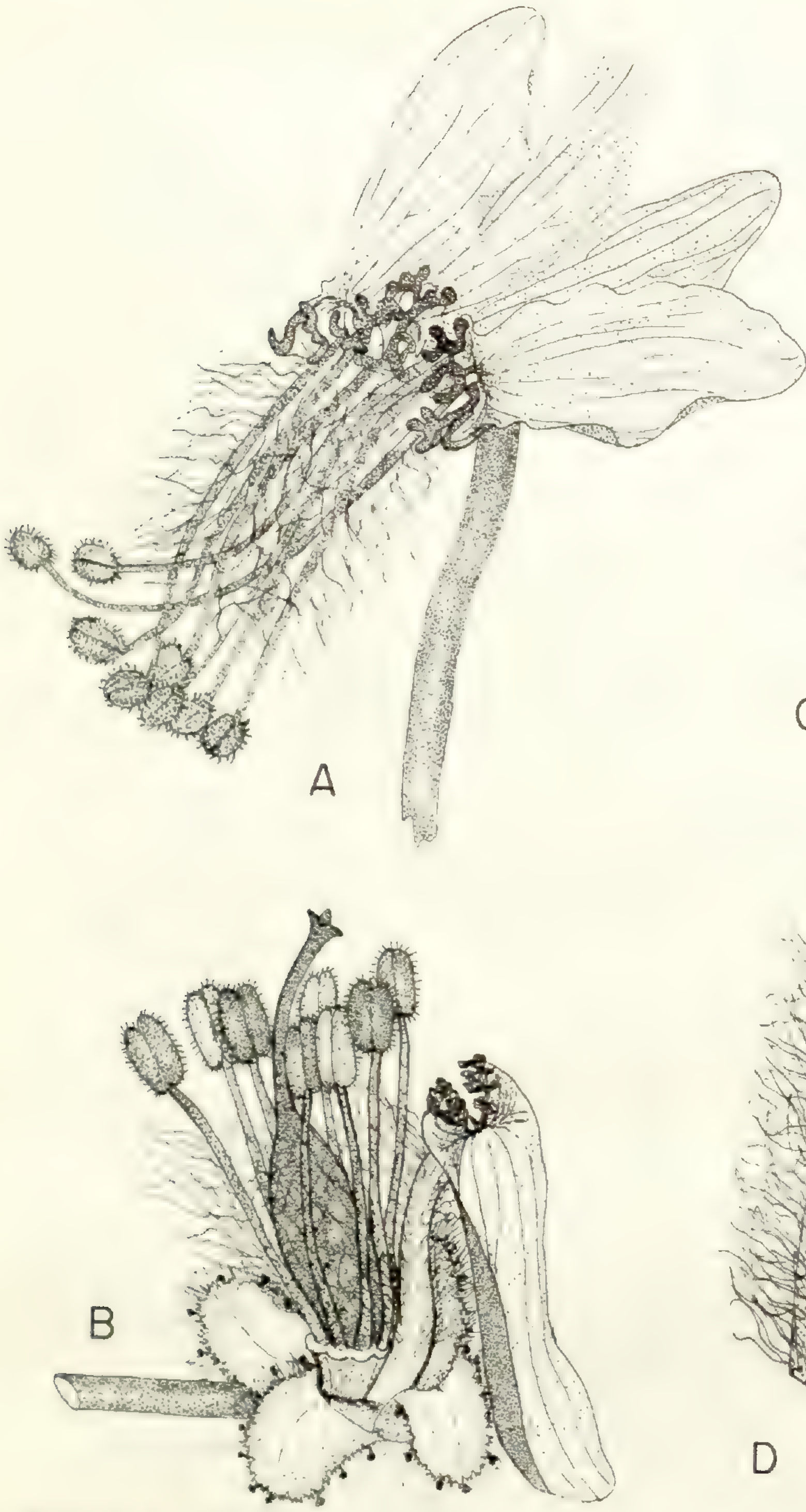

FIGURE 12. *Koelreuteria bipinnata*: A, staminate flower, × 7½; B, pistillate flower showing fimbriate-glandular calyx lobes, position of corolla lobe, sterile stamens, and young capsule, × 7½; C, corolla lobe (ventral side), showing villous claw and limb with basal appendages, × 15; D, corolla lobe (dorsal side), × 15.

California Bot. Gard., Los Angeles, *McClintock s.n.* (CAS); street tree, 1523 Castillo St., Santa Barbara, *Moran 2612* (SBBG); residential planting, 403 No. San Gabriel Blvd., Los Angeles Co., *Spalding s.n.* (CAS, NA); Hillside Park, Santa Barbara, *Van Rensselaer 1296* (SBBG); Franceschi Park, Santa Barbara, *Van Rensselaer 1314* (SBBG, UC). FLORIDA: Fairchild Tropical Garden, *Gillis*

8550 (A, NA). PENNSYLVANIA: Arboretum of the Barnes Foundation, *Fogg s.n.* (NA); F. D. Moore & Sons, nursery, Narberth, *Meyer & Mazzeo 12572* (NA).

Koelreuteria bipinnata, as the basionym and valid name for the species, has been confused by botanists and horticulturists with *K. integrifoliola*, a name first applied by E. D. Merrill for the "second representative of the genus to be found in Kwangtung Province, rather strongly characterized by its entire leaflets." However, as the present study has shown, plants with entire leaflets are not entirely restricted to Kwangtung, but, in fact, occur on a random basis and in varying degrees throughout the known distribution of *K. bipinnata*. Sometimes both entire and serrate leaflets may occur on the same branch, as in *E. H. Wilson 1609* and *Tsang 28321*, although more often herbarium specimens show material with either entire or serrate leaflets, reflecting more the collector's choice of material than the variation in a given plant. Furthermore, observations by Dr. John M. Fogg, Jr. (pers. comm.) have shown that a plant labeled *K. integrifoliola* at the Arboretum of the Barnes Foundation at first appeared with entire leaflets but later, during the course of development, produced leaves with serrate leaflets. This change seems to suggest an expression of latent juvenility, since we know that seedlings of this plant produce leaflets with strongly serrate margins. In any case, the name *K. integrifoliola* is without a firm taxonomic base.

Koelreuteria bipinnata has also been confused with *K. elegans* from Taiwan, although the two are clearly separable on discrete morphological grounds (see TABLE 1).

TABLE 1. **Characters distinguishing K. bipinnata from K. elegans.**

CHARACTER	*K. bipinnata*	*K. elegans*
LEAFLETS	weakly oblique, acute to short-acuminate; dull green above, veins obvious, especially in living plants	usually strongly oblique, sometimes caudate; smooth and lustrous above, veins barely obvious in living plants
CALYX LOBES	fimbriate-glandular	ciliate-glandular
PETALS	4, rarely 5	5 or 4
CAPSULES	valves 3.7–6.6 cm. long, 3–5 cm. wide	valves 3.4–5(–6) cm. long, (2.5–)3.1–4.6 cm. wide
DISTRIBUTION	southern China	Taiwan and Fiji

VERNACULAR NAMES. *Feng-chui-kuo* (Yunnan, fide *Feng 12611*); *Fu Yu Yeh Luan Shu*, bipinnate leaf Luan tree; *Hua Ch'iu Shu* (Hunan); *P'ao Hua Shu Hsing-shan*, bubble-flower tree (Hupeh); *Un Tsing-pa'ko* (Kwangtung, fide *Tsoong 1066*); *Shan Ts'o* (Cantonese).

GARDENS. According to Riedel (1957), *Koelreuteria bipinnata* was introduced into the United States in 1911 by Dr. Francesco Franceschi of Santa Barbara, California. The species is now also grown in Florida, and recently it was introduced to the mid-Atlantic region of the eastern United States, where it appears to be completely hardy in Philadelphia and Washington, D. C. It is also cultivated in China, Japan, and Egypt. Seeds of *K. bipinnata* were sent to France by Delavay in 1887 from Yunnan; however, the plant never became established in Europe, although it was offered at least once in the trade by Simon-Louis, Cat. 44 (1908). Until recently, the Earl of Rosse, who lives in Ireland, had the only living plant of *K. bipinnata* known to exist in Europe.[5]

3. **Koelreuteria elegans** (Seem.) A. C. Sm. in Contr. U. S. Natl. Herb. 30: 518. 1952; Parham, Pl. Fiji Islands 174. 1964.

Tree 7–25 m. in height, to ca. 50 cm. (2 m. recorded in Taiwan) in diameter; lenticels round to lens-shaped, pustulate, corky, cinnamon-brown; bark peeling in square plates, rough, somewhat corky, furrowed lengthwise. Leaves bipinnate, the odd terminal leaflet absent or much reduced, 25–60 cm. long, 15–44 cm. wide; rachis glabrous or short-hairy on the more or less grooved upper side; leaflets 8–17 on the major leaf divisions, strongly oblique, smooth and lustrous with barely manifest veins above, lanceolate to narrowly ovate to elliptic, 5.5–9.2(–10.2) cm. long, 1.3–3(–4.2) cm. wide, entire to irregularly crenate-serrate, long-acuminate to caudate at the tip, glabrous or with scattered straight hairs on the veins above and on petiolule, midvein beneath sparsely hairy with tufts of hairs in the axils and often with glands interspersed on the midvein and veinlets, sessile or with petiolules to ca. 3 mm. long. Inflorescence 30–50 cm. long, 20–25 cm. wide, densely puberulent and glandular, especially at anthesis, less so in fruit; flowers mildly sweet-fragrant; calyx lobes ciliate-glandular; pedicels scattered-puberulent or glabrous; petals usually 5 or 4, rarely 6, limb 5.5–7 mm. long, 1.5–3.5 mm. wide, acute or obtuse to rounded, appendages lobulate-undulate, claw 2–5 mm. long, densely villous; stamens densely villous near base, 4.5–10.1 mm. long. Capsules ellipsoidal, the valves rotund to suborbicular (placenta continuous and nonwinged), 3.4–5(–6) cm. long, (2.5–)3.1–4.6 cm. wide, inner side lustrous, reticulate-veined, scattered-pubescent when young, becoming glabrous, deep rose-purple while young, brownish at maturity; styles (1.5–)2–6 mm. long; seeds pyriform to nearly spherical, 5.2–5.5 mm. in diameter, black, slightly rugose or smooth.

DISTRIBUTION: Taiwan and Fiji.

Koelreuteria elegans manifests an interesting and puzzling distribution, with one element in Taiwan and the other in Fiji, a discontinuity of 7200 km. without a known intermediate station. The existence of a

[5] Recently, through a reliable source, I learned of the existence of *K. bipinnata* at La Mortola, a garden near Ventimiglia, Italy.

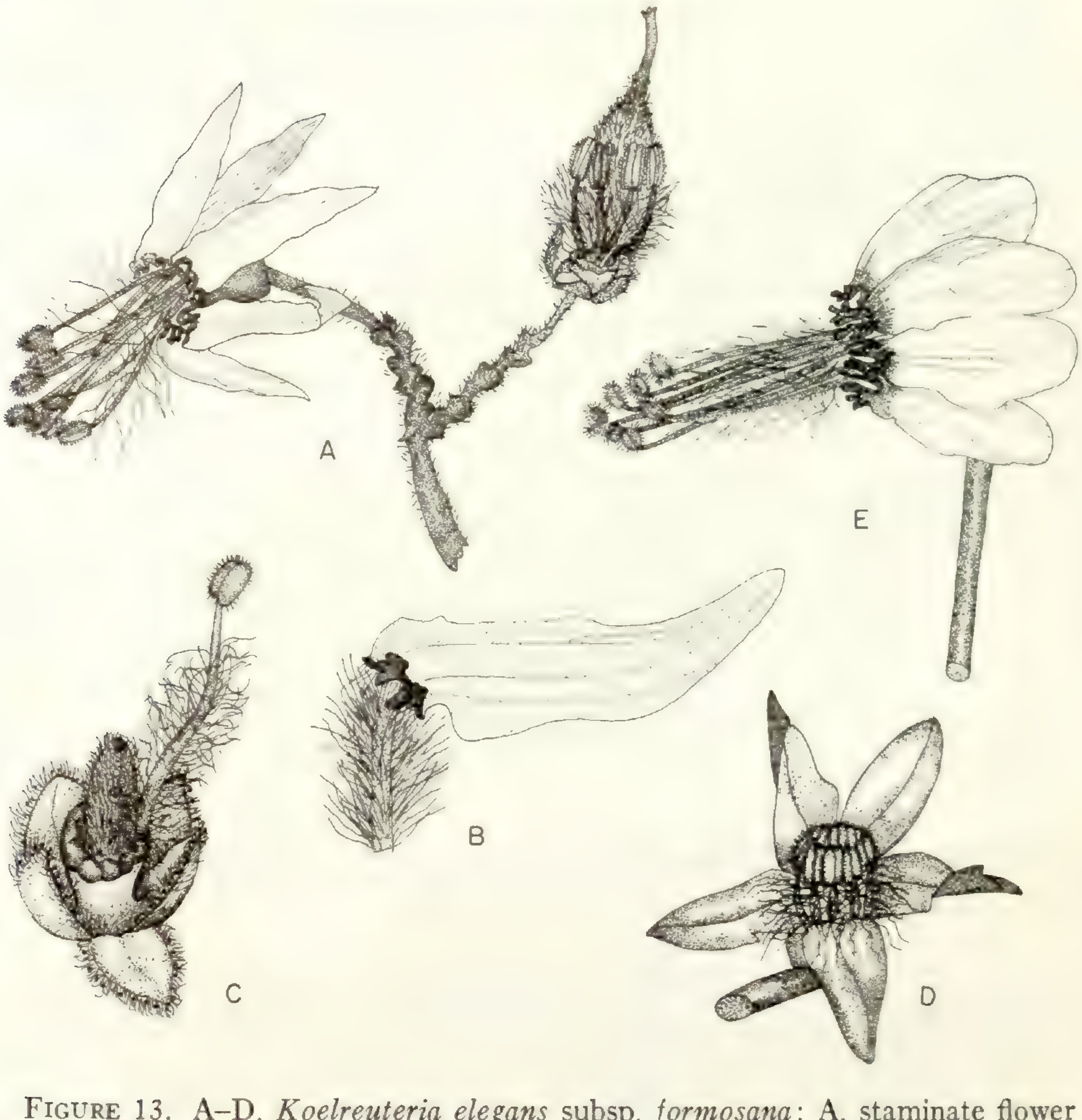

FIGURE 13. A–D, *Koelreuteria elegans* subsp. *formosana*: A, staminate flower (left) and pistillate flower (right) on ultimate branch of inflorescence, × 5; B, corolla lobe (dorsal side), showing the villous claw and limb with basal appendages, × 10; C, staminate flower, showing ciliate-glandular calyx lobes, disc on raised androgynophore, and stamen, × 5; D, staminate flower, showing whorl of 8 stamens which later become declinate, × 5; E, *Koelreuteria elegans* subsp. *elegans*, showing the broader obtuse corolla lobes and longer filaments, × 5.

species of *Koelreuteria* on Fiji was first confirmed by Smith in 1942, on the basis of recent collections, although sometime later, in 1952, Smith recognized that Seemann had collected the plant as early as 1860 on Vanua Levu. Already, Smith (1950) had presented convincing evidence that from "the size and habitat of these trees one must suppose that they are indigenous, although the record causes an extraordinary extension of the known range of *Koelreuteria*, otherwise limited to eastern Asia and Formosa." Later, Smith (1955) listed *Koelreuteria* among 101 genera of flowering plants found primarily in Indo-Malaysia and eastern Asia, with distributions terminating in Fiji as the easternmost limit. Although Fiji is rich in species endemics, represented by about 70 per cent of the flora, *K. elegans* is not one of them.

In spite of the wide geographic disparity, the two disjunct elements of *Koelreuteria elegans* are closely related. In their general *facies*, they are more alike than they are different, for although they differ consistently in minor details of the flowers and leaves, they do not differ significantly as to pollen morphology (see Dr. Nowicke's section on pollen morphology). Taxonomically, these geographically disjunct elements are treated at the subspecific level, a course which tends to emphasize their biologic affinities more fully than if they were treated separately as species. Intensive field study, no doubt, would help to clarify this point.

KEY TO THE SUBSPECIES OF KOELREUTERIA ELEGANS

A. Leaflets entire or sparsely serrate; petiolules 1–2.5(–3) mm. long; petals usually 4 or 5, rarely 6, obtuse to rounded, 5.5–7 mm. long, 2.7–3.5 mm. wide, claw 2.5–5 mm. long, up to twice as long as the calyx lobes, densely villous; filaments 8–10.1 mm. long; styles 4.5–7.5 mm. long. Fiji. . . . . 3a. subsp. *elegans*.

A. Leaflets often rather coarsely serrate; petiolules 4–5(–10) mm. long; petals usually 5 or 4, acute, 6–7 mm. long, 1.5–2.5 mm. wide, claw ca. 2 mm. long, slightly longer than the calyx lobes, sparsely villous; filaments 4.5–6 mm. long; styles 3–4(–5) mm. long. Taiwan. . . . . 3b. subsp. *formosana*.

3a. **Koelreuteria elegans** (Seem.) A. C. Sm. subsp. **elegans**.

FIGURES 6, 7, 13E–15.

Melia(?) elegans Seem. Fl. Vit. 36. 1865. HOLOTYPE: *Seemann 64* (K); isotype (GH).

Koelreuteria elegans (Seem.) A. C. Sm. in Contr. U. S. Natl. Herb. **30:** 518. 1952; Parham, Pl. Fiji Islands 174. 1964.

Koelreuteria formosana sensu A. C. Sm. in Sargentia **1:** 55. 1942; non Hayata, 1913.

Koelreuteria vitiensis A. C. Sm. in Jour. Arnold Arb. **31:** 299. 1950. HOLOTYPE: *Smith 4389* (A); isotypes (A, BISH, L, NY, P, US).

Leaflets 5.5–9.2 cm. long, 1.3–3 cm. wide, entire or sparsely serrate, acuminate to caudate, rarely acute (supernumerary leaflets like those in subsp. *formosana* absent); petiolules 1–2.5(–3) mm. long; petals usually 4 or 5, rarely 6, obtuse to rounded, 5.5–7 mm. long, 2.7–3.5 mm. wide, claw 2.5–5 mm. long, up to twice as long as the calyx lobes, densely villous; filaments 8–10.1 mm. long; styles 4.5–7.5 mm. long.

DISTRIBUTION. Fiji. Known to occur only on the two main islands of Vanua Levu and Viti Levu, where it flowers from the end of March to about the first of May. Fruiting occurs from the end of May to mid-July.

Various habitats have been recorded, including dry secondary forest used as pasture, rocky soils on ridges in open forest, clearings in low altitude forest edge, dry hillsides, slopes of escarpment, hillside thickets, and montane forest. It occurs at altitudes from about 350 m. to about 900 m.

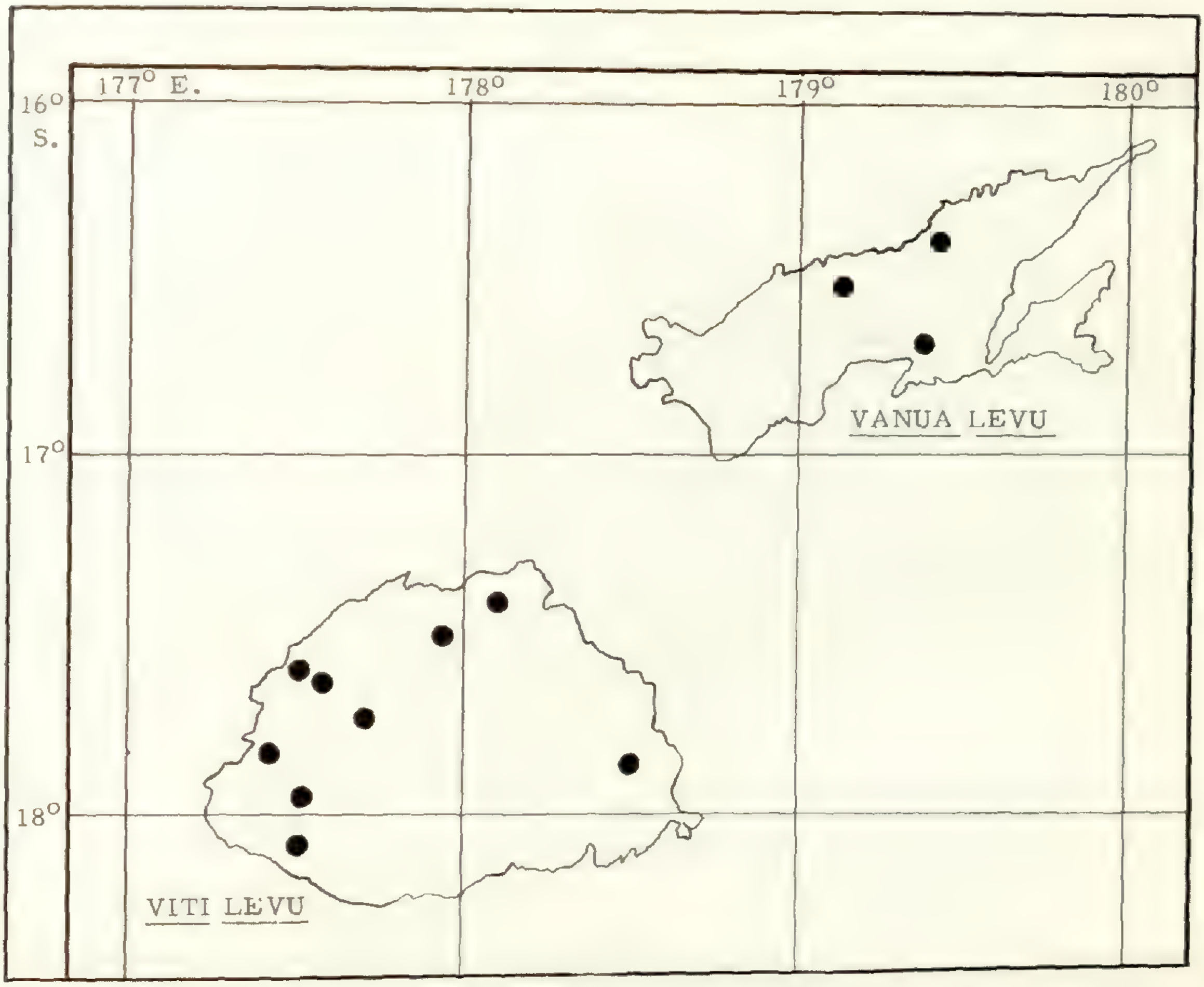

FIGURE 14. Distribution map of *Koelreuteria elegans* subsp. *elegans*.

REPRESENTATIVE SPECIMENS. **Fiji.** VANUA LEVU: above Saivon Village, Macuata [16.36S, 179.09E], *Berry 24* (SUVA); Korotari, Macuata Prov., *Howard 382* (SUVA); Drawa, Cakaudrove (Thakaundrove) [16.40S, 179.25E], (*Kurovoli*) *Fiji Dept. Agr. 14327* (BISH, K, NA, SUVA); Macuata coast, *Seemann 64* (K, holotype; isotype, GH); Mathuata, so. slopes of Mt. Numbuiloa, east of Lambasa [16.24S, 179.26E], *A. C. Smith 6429* (A, L, S, SUVA, US). VITI LEVU: Ra, vicinity of Rewasa, near Vaileka [17.24S, 178.11E], *Degener 15435* (A, BISH, BM, K, L, MO, NY, S, UC, US, W); Nadarivatu, trail around escarpment back of government station [17.39S, 177.35E], *Gillespie 4181* (BISH); Mts. near Lautoka [17.37S, 177.28E], *Greenwood 450* (K); Tholo North, below Nandarivatu, *Greenwood 450A* (A, NY, PH, UC, US); Naloto Range, Mba Prov. [17.43S, 177.44E], (*Koroiveibau & Qoro*) *Fiji Dept. Agr. 14778* (BISH, K); Vaniyasi (Nadi), Mba Prov. [17.49S, 177.27E], (*Labaliba*) *Fiji Dept. Agr. 2359* (SUVA); Singatoka Dist., head of Sovi Creek, *W. Parham 4* (K); Raskulu, near Kalavokoro, Nokonoko Dist., *H. B. R. Parham 250* (BM); King's Road [17.50S, 178.30E], *B. E. Parham 1213* (A, SUVA); Na Coco Levu, near Singatoka, Prov. Nadroga [18.11S, 177.31E], *W. L. Parham & H. B. R. Parham 301* (K); Nubulekaleka, Mba Prov., (*Qoro*) *Fiji Dept. Agr. 14725* (SUVA); Nadroga & Navosa, Nabosewale, vicinity of Nadrau [17.43S, 177.57E], (*Ranamu*) *Fiji Dept. For. 1171* (BISH, SUVA); Nadroga & Navosa, Tovua, Nabutautau [17.47S, 117.55E], (*Ranamu*) *Fiji Dept. For. 1191* (BISH, NA, SUVA); slopes of Mt. Nairosa, eastern flank of Mt. Evans Range, Mba Prov. [17.39S, 177.35E], *A. C. Smith 4389* (A, BISH, L, NY, P, US); Wainabuka valley, Naradrivatu [17.50S, 178.21E], *Vaughan 3437* (BM, K, US).

FIGURE 15. *Koelreuteria elegans* subsp. *elegans*: habit ((*Ranamu*) *Fiji Dept. For. 1171*), capsules and seed ((*Ranamu*) *Fiji Dept. For. 1185*), all × ¼.

The original material collected by Seemann was sterile. His notes (1865) referred to "a tree 24 feet high, having somewhat the habit of *M.* [*Melia*] *Azedarach*" and stated that while he was collecting his specimens, "the tree was just beginning to make new leaf, and had no flowers." Presumably the trees in Fiji are nearly leafless at the end of the dry season, and new growth was just beginning when Seemann visited the Mathuata coast of Vanua Levu during October of 1860.

As to the occurrence of *Koelreuteria elegans* subsp. *elegans* on Fiji, Smith (1950) noted the following: "In the Mt. Evans Range of northwestern Viti Levu, this tree is one of the most striking components of the vegetation during its short flowering season, which lasts for only about two weeks, in May or early June. From the high ridges one may observe large individuals, spectacularly covered with bright yellow flowers, in the forest on the inaccessible slopes."

The Fijian subsp. *elegans* differs from subsp. *formosana* in having leaflets tending to be entire or sparsely serrate, smaller, and usually less numerous, with shorter petiolules, larger and obtuse petals, and the claw, filaments, and style all longer than in subsp. *formosana* (cf. TABLE 2).

TABLE 2. **Characters distinguishing K. elegans subsp. formosana from subsp. elegans.**

CHARACTER	SUBSP. *formosana*	SUBSP. *elegans*
LEAFLETS	(4.5–)6–10 cm. long, 1.8–3(–4.2) cm. wide; average 13.5 leaflets	5.5–9.2 cm. long, 1.3–3 cm. wide; average 11.8 leaflets
PETIOLULES	4–5(–10) mm. long	1–2.5(–3) mm. long
PETALS	5 or 4; 6–7 mm. long, 1.5–2.5 mm. wide, acute	4 or 5, rarely 6; 5.5–7 mm. long, 2.7–3.5 mm. wide, obtuse
CLAW	ca. 2 mm. long	2.5–5 mm. long
FILAMENTS	4.5–6 mm. long	8–10.1 mm. long
STYLES	3–4(–5) mm. long	4.5–7.5 mm. long

The pollen with irregularly striate ektexine appears to be the most distinctive among the members of the genus examined by Dr. Nowicke (see section on pollen morphology), although it must be pointed out that the examination was based upon only one collection.

VERNACULAR NAMES. *Towiwi*, Mba Prov. (*W. Parham 4*); *Tatage*, Vanua Levu (*Berry 24*); *Wi Wi*, Nandronga Prov., Viti Levu (*H. B. R. Parham 250*); *Lomblomba*, Ra dialect (*Degener 15435*); *Manawi* (*Monawi*), Tailevu Prov., Viti Levu (*B. E. Parham 1213*).

USES. The Fijians use *Koelreuteria elegans* subsp. *elegans* in various ways. The Kai Viti make *manawi* (also spelled *monawi*), used as hair dye, from the leaves (*W. Parham 4*). Degener reports that a black dye is made by boiling the leaves and pouring the liquid over the hair (*Degener 15455*). It is interesting to note the similar use of the leaves for a black dye in both Fiji and China. The tree is also sometimes used for timber ((*Ranamu*) *Fiji Dept. For. 1171, 1185*).

GARDENS. *Koelreuteria elegans* subsp. *elegans* is occasionally cultivated in Fiji. In 1974, seeds of the Fijian plant were distributed to botanical gardens in California, the Gulf Coast, and Florida.

3b. Koelreuteria elegans subsp. **formosana** (Hayata) F. G. Meyer, comb. nov. FIGURES 13A–D, 16.

Koelreuteria formosana Hayata, Icon. Pl. Formosan. 3: 64, 65. *pl. XIII.* 1913; Ito, Ill. Fl. Formosa 566. *fig. 564.* 1927; Sasaki in Trans. Nat. Soc. Formosa **19:** 410. 1929; Radlk. in Engler, Pflanzenr. **IV. 165:** 1334. 1933. HOLOTYPE: *Kawakami & Mori 1736* (TAIF; photos, A, NA, UC, US).

Koelreuteria bipinnata sensu Henry in Trans. Asiatic Soc. Japan **24**(suppl.): 128. 1896; sensu Matsumura & Hayata in Jour. Coll. Sci. Imp. Univ. Tokyo **22:** 94. 1906; non Franchet, 1886.

Koelreuteria henryi Dümmer in Gard. Chron. 3rd ser. **52:** 148. 1912; Elwes & Henry, Trees Gr. Brit. & Ireland **7:** 1931. 1913; Radlk. in Engler, Pflanzenr. **IV. 165:** 1332. 1933. HOLOTYPE: *Henry 1594* (K); isotype (A).

Leaflets (4.5–)6–10.2 cm. long, 1.8–3(–4.2) cm. wide, often rather coarsely serrate, long-acuminate to caudate (supernumerary small leaflets occasionally occur at the proximal end of the rachis); petiolules 4–5(–10) mm. long; petals usually 5 or 4, acute, 6–7 mm. long, 1.5–2.5 mm. wide, claw ca. 2 mm. long, slightly longer than the calyx lobes, sparsely villous; filaments 4.5–6 mm. long; styles 3–4(–5) mm. long; $2n = 22$ (Bowden, 1945).

DISTRIBUTION. Taiwan; also cultivated in gardens. *Koelreuteria elegans* subsp. *formosana* is apparently fairly widespread in Taiwan; however, little is known about the abundance and altitudinal range of this taxon owing primarily to a paucity of herbarium material with good data. Reputedly this is a tree of low elevations, although none of the material at my disposal mentions altitude. Flowering in September and October; fruiting in November.

REPRESENTATIVE SPECIMENS. **Taiwan.** Bankinsing Mts., *Henry 1594* (K, holotype of *K. henryi*; isotype, A); Nanto Hokuzanko, *Ito 15815* (TAIF); Tappanzan, Toyen [24.50N, 121.21E], *Kanahira & Sasaki s.n.* (A); Mt. Kakuban [24.50N, 121.21E], *Kanahira & Sasaki s.n.* (TAIF); Tappansha, Kagi, *Kawakami & Mori 1736* (TAIF, holotype; photos, A, NA, UC, US); Cuntin, Hunchuen, *Keng s.n.* (A, E, US); Paiwan, *Matuda 072082* (TAI); Kaohsiung, *I. Sasaki s.n.* (TI); Taihoku [24.50N, 121.21E], *I. Sasaki s.n.* (TAI); Saisho Kauirashi [23.11N, 120.17E], *J. Sasaki s.n.* (TAIF); upper Pinan River, Prov. Pinan, *E. H. Wilson 11145* (A, K); Lian-Hwa-Chih, Nan-Tou (as seeds), *NA 35210* (NA); Chung-pu, Chia-yi (as seeds), *NA 35211* (NA); Tai-ma-lee, Tai-tung (as seeds), *NA 35212* (NA); Tai-chung City (as seeds), *NA 35209* (NA).

CULTIVATED. **Africa: Egypt.** Agricultural Museum garden, Dokko, Giza, *Mahdi s.n.* (CAI, NA); Faculty of Agriculture garden, Giza, *Drar s.n.* (CAI, NA). **Rhodesia.** Grove Farm on Umwindsi River, Goromonzi Dist., *Biegel 4231* (NA). **Australia.** QUEENSLAND: Hamilton, Brisbane, in ground of Butter Marketing Board, *L. P. King s.n.* (K). **Asia: Taiwan.** Campus, National Taiwan University, Taipei, *Keng s.n.* (TAI); Taihoku [Taipei] cult., *I. Sasaki s.n.* (TAI); First Government Exp. Farm, *Sekyo-Sai 072081* (TAI). **North America: U.S.A.** ALABAMA: Tom Dodd Nursery, Semmes, Mobile Co., *Meyer & Mazzeo 11145* (NA). CALIFORNIA: Upper Orpet Park, *Broder s.n.* (NA); Hugh Evans' place, Santa Monica, *Eastwood s.n.* (A); West Los Angeles, *Epling s.n.* (CAS); Los Angeles State & County Arboretum, *Jativa 2265, 2267* (NA); University Arboretum,

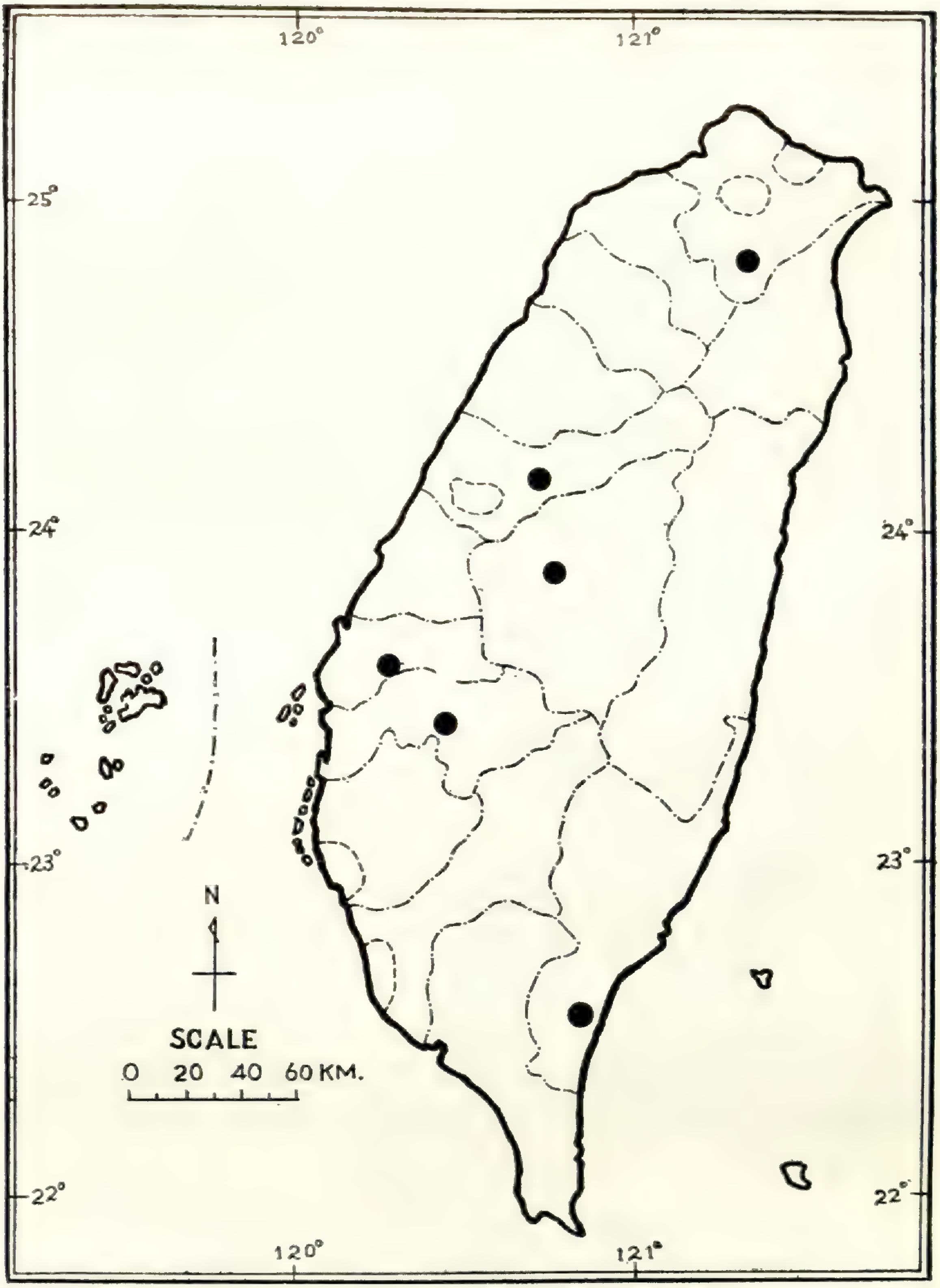

FIGURE 16. Distribution map of *Koelreuteria elegans* subsp. *formosana*.

Davis, *McClintock s.n.* (CAS, NA); 1111 Mission Ridge Road, Santa Barbara, *Moran 2599* (SBBG); University of California campus, Davis, *McClintock & Leiser s.n.* (CAS). FLORIDA: 10400 Old Cutler Road, Coconut Grove, *Avery 1035* (NA); Captiva Island, Lee County, *Brumbach 6029* (A); Fairchild Tropical Garden, Coconut Grove (P. I. 41679), *Gillis 8547* (A, CAS, NA, USF); U. S. Dept. Agr. Plant Introduction Station, Coconut Grove (P. I. 41679), *Gillis 11115, 11141* (CAS, NA); City Cemetery, Miami, Dade Co., *Korsakoff s.n.* (NA);

20 Fourteenth Ave., South Naples, *F. C. Lee s.n.* (A); Hort. ex H. Guy, Winter Haven, *Mazzeo 2383* (A, NA); The Wilmat, University of Florida, Gainesville, Alachua Co., *Meyer & Mazzeo 14220* (NA); Hort. ex W. Paul Philips, 316 E. Church St., Orlando, *collector undesignated* (A); roadside tree near my home, Altamonte Springs, Seminole Co., *Schallert 489* (BM, P, S, USF). HAWAII: Vineyard St. Nursery, Honolulu, *Forbes s.n.* (BISH); Lyon Arboretum, *Herbst 641* (BISH); Foster Gardens, Honolulu, *Neal s.n.* (BISH). LOUISIANA: Hort. ex 104 W. William David Pkwy., Metairie, *Painter s.n.* (USF); Hort. ex Prytania St., corner Dufossat, New Orleans, *Ewan 22185* (NA); arboretum, University of Southwestern Louisiana, Lafayette, *Solymosy SC01109702* (NA). MISSISSIPPI: Poplarville, *Rogers 8680* (NA). TEXAS: campus of Texas A & M University, Brazos Co., *Fryxell 1215* (US); Corpus Christi, *F. G. Meyer s.n.* (NA, photo); Rice Institute Campus, Houston, *Traverse 884, 1725* (MO); near corner of Gramercy and Stella Link, Houston, Harris Co., *Traverse 1724* (GH). **West Indies: Cuba.** Harvard Tropical Garden, Soledad, Cienfuegos, Prov. Santa Clara, *Jack 8347* (A, NY, US). **Europe: Italy.** Stazione Sperimentale di Floricoltura, San Remo, *collector undesignated* (K). **England.** Royal Botanic Gardens, Kew, *Bean s.n.* (K).

Koelreuteria elegans subsp. *formosana* differs from the Fijian subsp. *elegans* principally in the flowers with narrower acute petals, the filaments less villous and distinctly shorter, and the larger leaflets often more coarsely serrate than in subsp. *elegans* (see TABLE 2).

VERNACULAR NAMES. *Taiwan mokugenji*; *Taiwan Sendanbotaizgu* (*Matuda 072082*).

GARDENS. The earliest recorded introduction of *Koelreuteria elegans* subsp. *formosana* into the United States dates from an introduction by the United States Department of Agriculture (P.I. 41679) in 1915 from Taihoku [Taipei], Taiwan. This attractive tree is now grown in Hawaii, in California, and on the Gulf Coast; in Florida it has escaped from cultivation in certain areas. Flowering occurs from the end of September through October. During anthesis, the flowers emit a mild orange-blossom-like fragrance, which is highly attractive to bees and other pollinating insects.

EXCLUDED NAMES

Kölreutera mulluginoides Murray in Nov. Comm. Soc. Sci. Gott. 3: 67. *tab. II. pl. 2.* 1773 = **Gisekia pharnacioides** L.

Koelreutera hygrometrica Hedwig, Fundam. Muscor. 2: 95. 1782 = **Funaria hygrometrica** Hedwig.

Koelreutera Schreb. Gen. 2: 731. 1791.

Koelreuteria arborea Blanco, Fl. Filip. (ed. 3) 4: (Nov. App.) 52. 1880 = **Guioa perrottetii** (Bl.) Radlk.

Koelreuteria arborescens Pierre nom. in hb. = **Arfeuillea arborescens** Pierre.

Koelreuteria completa Medic. in Hist. & Comm. Acad. Elect. Sci. Theod. Palat. VI. 407. 1790 = **Marsdenia erecta** R. Br?

Koelreuteria edulis Blanco, Fl. Filip. (ed. 2) 202. 1845; (ed. 3) 4: (Nov. App.) 52. *pl. 110*. 1880 = **Otophora fruticosa** (Roxb.) Bl.
Koelreuteria incompleta Medic. in Hist. & Comm. Acad. Elect. Sci. Theod. Palat. VI. 407. 1790 = **Marsdenia erecta** R. Br?
Koelreuteria procumbens Medic. Bot. Beobacht. 22. (1782) 1783 = **Marsdenia erecta** R. Br?
Koelreuteria triphylla nom. in hb. P–Jussieu (n. 11345) = **Urvillea ulmacea** Kunth.
Koelreuteria minor Hemsley in Hooker's Icon. Pl. 27: *pl. 2642*. 1900; non *Koelreuteria*.

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THE OLD WORLD SPECIES OF CALOPHYLLUM (GUTTIFERAE). 1. THE MASCARENE SPECIES

P. F. STEVENS

THIS ACCOUNT OF the genus *Calophyllum* L. in the Mascarenes (Mauritius, Réunion, and Rodrigues) is necessary to establish the nomenclature of the species for the *Flore des Mascareignes* currently being prepared jointly by Kew, O.R.S.T.O.M. (Paris), and M.S.R.I. (Mauritius). The nomenclatural problems have been entirely disproportionate to the area covered and the number of species involved, and one name, *C. acuminatum* Lamarck, has been excluded from the genus (p. 181). It was hoped that a joint account of the Madagascan and Mascarene species could be prepared; however, the species of Madagascar have proved more complex than expected.

Although only three species of *Calophyllum* are native to the Mascarenes, they are of considerable interest; the species that are not found, but might be expected, are of almost equal interest. There are about 14 native species of *Calophyllum* on Madagascar, but none of these are native to the Mascarenes; however, both *C. inophyllum* L. and *C. recedens* Jumelle & H. Perr. seem to be related to the Mascarene species *C. tacamahaca* Willd. *Calophyllum inophyllum*, perhaps rather surprisingly, does not appear to be native to the Mascarenes, although it is common in parts of Madagascar and is found in the archipelagoes between Madagascar and India. The two species endemic to Mauritius, *C. parviflorum* Baker and *C. eputamen* sp. nov., are unique in the genus in lacking any woody layer in the ripe fruit, although a thin woody layer is present in the immature fruit. Information on the germination and dispersal of these species would be of interest.

In the account that follows, the following abbreviations have been used for collections made as part of an institutional series: *SF* — Service Forestier (Madagascar) and *MAU* — Flora of Mauritius. Herbarium abbreviations follow those given by Holmgren and Keuken, *Index Herbariorum*, ed. 6, 1974; REU is used as an abbreviation for the "Herbier du Centre d'Enseignement Superieur Scientifique (la Réunion)."

KEY TO THE TAXA OF CALOPHYLLUM IN THE MASCARENES

1. Tomentose indumentum on terminal bud, young stem, and base of the inflorescence; venation fine and dense; tepals 4. ..... 4. *C. soulattri.*
1. Tomentose indumentum absent; venation not fine and dense; tepals 8 or more.
   2. Lamina with 5–8(–10) veins/5 mm.; lowest internode of inflorescence usually less than 0.5 mm. long; fruit with a stone rounded at the apex. ..... 2. *C. inophyllum.*

2. Lamina with (5–)7–15 veins/5 mm.; lowest internode of inflorescence usually 0.6–3 cm. long; fruit lacking a stone, or stone pointed at apex.
   3. Lamina usually acute to acuminate; fruit with stone wall ca. 1 mm. thick. ..... 5. *C. tacamahaca.*
   3. Lamina usually rounded to retuse; fruit lacking a stone when mature.
      4. Lamina 2.5–5.5(–7.5) cm. long; outer layer of fruit 0.4(–1) mm. thick. ..... 3. *C. parviflorum.*
      4. Lamina (5.7–)7–17.5 cm. long; outer layer of fruit (2–)3–3.5 mm. thick.
         5. Terminal bud 4.5—7 mm. long; petiole 5–10 mm. long; lamina 5.7–10.5 cm. long. ..... 1. *C. eputamen* var. *eputamen.*
         5. Terminal bud 8–10 mm. long; petiole 8–15 mm. long; lamina (7–)9.5–17.5 cm. long. ..... 1. *C. eputamen* var. *grandis.*

1. **Calophyllum eputamen** P. F. Stevens, sp. nov.

E speciebus aliis Calophylli (*C. parvifloro* excepto) in fructu maturo sine putamine differt, et a *C. parvifloro* in foliis maioribus (eis *C. parviflori* minus quam 7.5 cm. longis et 4.8 cm. latis), costa latioribus, floribus maioribus, et fructibus duplo maioribus stratis exterioribus (?2–)3–3.5 mm. crassis (in *C. parvifloro* solum circa 0.4(–1) mm. crasso) differt.

Arbor 5–6 m. alta trunco usque ad 30 cm. in diametro. Gemma terminalis corpulens, 4.5–7 mm. longa, indumento breve griseo tegenti compacto facienti praedita; ramulus haud vel leviter complanatus 2.5–5 mm. in transverso, 4-angulatus, glaber, in siccitate brunneus vel atrobrunneus; internodia 0.3–2 cm. longa. Petiolus 0.5–1.0 cm. longus et 3.5–5 mm. latus, supra late vadoseque concavus, infra convexus, glaber; lamina late obovata, elliptica vel subrotunda, raro ovata, 5.7–10.5 cm. longa et 3.9–8 cm. lata, apice rotundata vel retusa basi cuneata vel acuta in petiolo decurrens, maturitate glabra, coriacea, in siccitate utrinque flavo-brunnea vel griseo-brunnea, margine haud undulata plus minusve recurvata, costa utrinque e basi sensim angustata, plana vel leviter elevata, striata, (0.8–)1.5–3 mm. lata in medio laminae, saepe circa 5 mm. ante apicem evanescenti, nervis lateralibus supra obscuris vel subprominulis infra prominulis elevatis 6–11 per 5 mm. sub angulo 60–70° e costa divergentibus. Inflorescentiae e axillis foliatis ortae, rarissime terminales, cum 9–17 floribus; axes 4.5–11 cm. longi, glabri, floribus infimis 0.5–3 cm. supra bases ortis, haud ramosi; bracteae foliaceae late ovatae vel subrotundae, subpersistentes, 0.3–2 cm. longae, infra indumento subfurfuraceo praeditae; pedicellus 0.9–3.4 cm. longus, glaber. Flos hermaphroditus; tepala 8–12 (–13), duobus exterioribus subrotundis vel late ovatis 6.5–10 mm. longis et 5–9 mm. latis, glabris vel pilis brevibus fimbriatis, tepalis interioribus ellipticis vel obovatis 9–13 mm. longis et (1.5–)3.5–9 mm. latis (tepalis intimis multo parvioribus quam praesertim duobus exterioribus); stamina 270–410, filamentis usque ad 7.5 mm. longis basi usque ad 1 mm. connatis, antheris oblongis 1.3–2 mm. longis apicibus plus minusve truncatis; ovarium 2–2.7 mm. longum, glabrum; stylus 4–5.5 mm. longus; stigma peltata, 1.2–1.7 mm. in transverso, cum (2–)4 lobulis. Fructus ellipsoi-

deus vel ovoideus usque ad 4 cm. longus et 2.4 cm. latus interdum basi styli persistenti praeditus, in siccitate brunneus, rugosis subtilibus vadosis praeditus; stratum exterior (?2–)3–3.5 mm. crassum compactum (apice basique circa 7.5 crassum); strata lignosum et spongiosum nulla; embryo circa 2.2 cm. longus et 1.5 cm. latus.

TYPE: Mauritius, Pétrin, 600 m., 3 Dec. 1973, *Coode 4263* with *Guého & Badré* (holotype, K; isotype, A).

ADDITIONAL SPECIMENS SEEN. **Mauritius:** near Pétrin, *MAU 16666* coll. *Forestry Dept.* (MAU); Pétrin, ca. 450 m., *Coode 3951* with *Guého & Lorence* (A, K); Grand Bassin, *Vaughan s.n.* Jan. 1940 (MAU), *Colville s.n.* (E, 2 sheets), *anon.* (K); Plaine Sophie, Plaine Champagne, *MAU 27* (MAU); à l'est de la forêt de Maccabée, *28262 SF* coll. *Capuron* (P); Mare Longue–Maccabée Road, *MAU 13301* coll. *Vaughan* (MAU); track from Les Mares to Cocotte Mt., *MAU 10710* coll. *Vaughan* (MAU); *sine loco, Franco-British Exhibition* (K), *Commerson s.n.* (P, P–JU *11882*), *Bouton s.n.* (K), *MAU 3054* coll. *Forestry Dept.* (MAU).

FIELD CHARACTERS. Bark light red-brown, fissured; inner bark red outside, paler pinkish straw toward the cambium. Latex yellow, clear.

ECOLOGY. *Calophyllum eputamen* var. *eputamen* grows in stunted forests and heathlands on very shallow soil in marshy conditions; it has been collected from altitudes of about 450 to 600 m. Specimens in flower have been collected from January to March, specimens in fruit in August and December. Fallen fruits are brown or black.

The leaves are sometimes galled, e.g., in *Coode 3951*. The galls are in a line ca. 0.5–1.3 cm. in from the edge of the leaf and consist of elliptic outgrowths from the surface of the lamina which sometimes distort the whole leaf.

LOCAL NAMES. "Tatamaka," "tatamaka à petites feuilles."

1a. C. eputamen var. grandis P. F. Stevens, var. nov.

Arbor circa 6 m. alta, trunco 12–20 cm. in diametro. Gemma terminalis 8–10 mm. longa; ramulus 3.5–6.5 mm. in transverso. Petiolus 0.8–1.5 cm. longus et circa 4 mm. latus; lamina elliptica, ovalis vel obovata, (7–)9.5–17.4 cm. longa et (3.3–)4.4–9.8 cm. lata, apice subretusa, rotundata vel obtusa, basi plus minusve decurrens, costa supra 0.9–2 mm. lata in medio laminae, infra plus minusve elevata, nervis 8–13 per 5 mm. sub angulo 65–75° e costa divergentibus. Fructus breviter ovoideus vel ellipsoideus, 2.4–3.5 cm. longus et 2–2.5 cm. latus. Aliter quam in var. *eputamen*.

TYPE: Mauritius, Bassin Blanc, 500 m., 6 Dec. 1973, *Coode 4290* with *Guého & Lorence* (holotype, K; isotype, A).

ADDITIONAL SPECIMENS SEEN. **Mauritius:** Bassin Blanc to Les Mares, 500 m., *Coode 4284* with *Guého & Lorence* (A), Grand Bassin, 716 m., *MAU 164* coll. *Vaughan* (MAU).

FIELD CHARACTERS. Bark yellow-gray, with vertical fissures 2.5–5 cm. apart when older; inner surface yellow-brown; under bark red, creamy under the cracks; inner bark salmon-pink, almost white near the cambium. Latex yellow, clear.

ECOLOGY. *Calophyllum eputamen* var. *grandis* is a sometimes common plant of valleys or of forests on windswept ridges, growing at altitudes of 500 to 720 meters. Regeneration is reported in disturbed valley forests. Fruiting specimens have been collected in December.

Calophyllum eputamen is related to *C. parviflorum*, differing most obviously in the larger size of all its parts, especially of the fruits (almost twice as large and with an outer layer about 5 times as thick). However, it should be noted that the description below of the ripe fruit of *C. parviflorum* is taken from a somewhat atypical specimen with very coriaceous leaves.

Four collections of *Calophyllum eputamen* var. *eputamen* which have habitat data mention that the plant was collected in swampy and marshy places. Var. *grandis* seems to grow in better drained places, and some of the differences between the two varieties may be directly caused by the environmental differences. Both varieties have the same very characteristic leaf and fruit type, and terminal inflorescences are also known from both varieties.

2. **Calophyllum inophyllum** L. Sp. Pl. 513. 1753; Bojer, Hort. Maurit. 51. 1837; Baker, Fl. Maurit. 16. 1877, *pro parte*. TYPE: description based on material from Ceylon.

C. bintagor Roxb. Hort. Bengal. 41. 1814; G. Don, Gen. Syst. **1**: 622. 1831; Roxburgh, Fl. Ind. ed. 2. [W. Carey, ed.] **2**: 607. 1832. TYPE: described from the Moluccas.

C. calaba auct. non L.; Lamarck, Encycl. Méth. Bot. **1**: 553. 1785, *pro parte*.

Tree 4–10 m. tall. Terminal bud rather plump, 4.5–6 mm. long, with short, sometimes subfurfuraceous, grayish or brownish indumentum; twigs slightly flattened, 3–5.5 mm. across, with 4 or 6 raised lines when young, drying brown, glabrous; internodes (0.5–)1.5–2.5(–5) cm. long. Petiole 1–1.8 cm. long, broadly concave above, convex below, glabrous; lamina elliptic to oval, rarely ovate, 9.5–19 cm. long and 4.6–11.5 cm. across, rounded to slightly retuse at apex, sometimes subacute, acute to cuneate at base, glabrous, ± chartaceous, drying greenish brown to brown above and below, margin slightly undulate, recurved, midrib above narrowing quickly near the base or gradually narrowed from the base, depressed, becoming ± raised toward the apex, 0.4–0.8 mm. wide at the midpoint, raised below, angled toward the apex, striate toward the base, venation prominulous to prominent above and below, 5–8(–10) veins/5 mm., angle of divergence (65–)70–80°. Inflorescences from foliate axils, 7–13-flowered, axis 2.5–6.5 cm. long, glabrous except for minute puberulence near the base, basal internode 0.2–0.5(–0.9) cm. long, unbranched,

flowers not flabellate; bracts unknown, caducous; pedicels 1.5–5 cm. long. Flowers hermaphroditic; tepals 8, rarely 10, at least the outer fringed with short hairs, outer two broadly ovate to suborbicular, 5.5–7 mm. long and 4.5–7 mm. across, next pair elliptic to obovate, 9.5–11 mm. long and 6–7 mm. across, inner tepals ± obovate, 10.5–14 mm. long and 3–5.5 mm. across; stamens 255–355, filaments to 7.5 mm. long, connate for up to 1.5 mm., anthers oblong, 1.2–2 mm. long, apex rounded to retuse; ovary 2–3 mm. tall, glabrous; style 6–9.5 mm. long; stigma peltate, 1–1.5 mm. across, not obviously lobed. Fruit subpyriform to spherical, ca. 2.5 cm. long and 2.2–2.5 cm. across, apex rounded to apiculate, drying grayish brown, rather densely and sharply wrinkled; outer layer detaching ± cleanly from the stone, ca. 1 mm. thick, ± compact (air spaces developing?); stone spherical to ellipsoid, 2.2–2.3 cm. long and 1.9–2.3 cm. across, apex rounded, walls ca. 1 mm. thick, smooth, unmarked; spongy layer prominent, to 2.7 mm. thick.

ADDITIONAL SPECIMENS SEEN. **Mauritius:** Baie du Cap, sea level, *Coode 4011* with *Guého* (K); Baie du Tombeau, *MAU 12560* coll. *Morin* (MAU); Port Louis, *Ayres s.n.* Dec. 1860 (GH, K); near Yemen Estate, Black River, *MAU 1263* coll. *Vaughan* (MAU); Belle Mare Estate, 0.8 km. from the sea, *MAU 12598* coll. *Rouillard* (MAU); "Riambel" near Souillac, *MAU 11607* coll. *Antoine* (MAU); embouchure Riv. St. Gilles, *MAU 96* (MAU); lowlands, *MAU 16665* coll. *Morin* (MAU); *sine loco*, *Bouton s.n.* anno 1864 (K). **Réunion:** la place de l'Église de St. Paul, *Cadet 4973* (K); littoral à St. Denis, *Cadet 4914* (K); Ste. Marie, *Cadet 5157* coll. *Etienne* (K). **Rodrigues:** above Port Mathurin, ca. 150 m., *Coode 4299* (A, K); St. Gabriel, 300 m., *Cadet 2778* (P); *sine loco*, *Bouton s.n.* (K), *Balfour s.n.* (BM, K).

ECOLOGY. *Calophyllum inophyllum* usually grows by the sea at low altitudes, although it may flourish inland when planted. Specimens in flower have been collected from December to March, a specimen in fruit in May.

LOCAL NAMES. "Takamaka de Madagascar" (Bojer, *loc. cit.*), "takamaka."

Calophyllum inophyllum is an easily recognizable species. It usually has a broad lamina with rather distant venation (5–8 veins/5 mm.), the twigs are stout, and the inflorescences bear flowers with long, slender pedicels. The grayish, sharply wrinkled, fallen fruits with their subspherical stones are a characteristic sight on the beaches where *C. inophyllum* grows.

The germination of the fruit of *C. inophyllum* in Australia and New Guinea has been described by Stevens (1974). Smith and Darwin (1974, fig. 6) included a good photograph of the characteristic fruit.

It is probable that *Calophyllum inophyllum* has been introduced in all three islands. Baker (*loc. cit.*) recorded it as being "common in the forests of the sea shore" on Mauritius, but this statement is belied by the paucity of the specimens from that area. Bojer (*loc. cit.*) noted that it was "presque naturalisée" on the island, and the local name that he gave for it, "takamaka de Madagascar," might suggest that it had been introduced

from Madagascar. Notes on several specimens suggest that the species is planted or growing in waste places (e.g., *Bouton s.n.* anno 1864, *MAU 16665*), although a note on *MAU 96* suggests that it is native. All of the specimens cited from Réunion came from planted trees, and *Coode 4249*, from Rodrigues, also came from a tree which was apparently planted. *C. inophyllum* regenerates naturally in the Mascarenes, at least on Mauritius and Rodrigues.

Calophyllum inophyllum is common on Madagascar, being most abundant along the northern part of the east coast, and it appears to be represented by the small-fruited form described as *C. inophyllum* var. *takamaka* Fosberg. The little fruiting material seen from the Mascarenes also had rather small fruits. However, the fruits were not mature, lacking the plugs at the base of the stone which are found in ripe fruits throughout the range of the species (see also Stevens, 1974). Although *C. inophyllum* has larger fruits in the eastern part of its range, there is considerable variation in fruit size even there, and the immaturity of the fruits from the Mascarenes makes it impossible to suggest a place of origin for the Mascarene *C. inophyllum*.

Calophyllum bintagor is one of the names validly published in Roxburgh's *Hortus Bengalensis* (Robinson, 1912). In a footnote Roxburgh referred to "H. A. 2 t. 71" — the illustration of *Bintangor maritima* in Rumphius, Herbarium Amboinense 2: tab. 71. 1741. Later Roxburgh mentioned that Rumphius's illustration was a poor representation of his *C. bintagor* (Roxburgh, *loc. cit.* 1832). *Bintangor maritima* is to be equated with *C. inophyllum*.

There is a sterile specimen of *C. bintagor* Roxb. at the British Museum which agrees well with the description given by Roxburgh (*loc. cit.* 1832); this specimen is clearly *C. inophyllum*. On one sheet is written "*C. Bintagor*," and on another "N 10 1811 8.19," the three groups of figures being under one another. As this writing is comparable to that on the sheets of another Roxburgh collection (see *C. lanceolarium* Roxb. below), the specimen of *C. bintagor* almost certainly came from Roxburgh.

Roxburgh (*loc. cit.* 1814) mentioned that *Calophyllum bintagor* had been sent to him by one Monsieur Jannet in 1810 and that it had come from the Moluccas. Later the specimen was mentioned as coming from Mauritius (Roxburgh, *loc. cit.* 1832). This Monsieur Jannet would seem to have been a much-travelled gentleman, since he is recorded as having sent specimens to Roxburgh in 1810 from America (*Acer negundo* L.), the West Indies (*Malachra capitata*), the Moluccas (*C. bintagor*), as well as Mauritius (*C. lanceolarium*), and his travels during the following year also span the globe (Roxburgh, *op. cit.* 1814). The person in question is probably V. F. Jaunet, who lived a long and checkered life on Mauritius (he ended up planting tea, but was ruined when governmental assistance was discontinued, and died at Port Louis in 1861). Presumably the material he sent was from the Botanic Garden in Mauritius, but although he is supposed to have sent plants to the Muséum d'Histoire Naturelle at Paris, I have not seen any material of *Calophyllum* there

collected by him. It may well be that the initial mention of the Moluccas as the source of the plants of *C. bintagor* is correct, since the status of *C. inophyllum* on Mauritius is at best doubtful.

3. **Calophyllum parviflorum** Bojer ex Baker, Fl. Maurit. 16. 1877; *C. tacamahaca* Willd. var. *parviflorum* (Bojer ex Baker) Vesque in DC. Monogr. Phanerog. 8: 548. 1893. TYPE: Mauritius, *herb. Justice Blackburn* (lectotype, K).

C. spurium auct. non Choisy; Bojer, Hort. Maurit. 52. 1837.

Shrub or tree 1.5–5 m. tall to 23 cm. d.b.h. Terminal bud hardly flattened, 4–6 mm. long, with short, gray-brown indumentum forming a compact dense covering; twig not or hardly flattened, 1–3 mm. across, with 4 or 6 raised lines, drying brown to dark brown, when young with sparse brownish subfarinose indumentum, glabrescent; internodes 0.2–1 cm. long. Petiole 3–7 mm. long, 1–2 mm. wide, broadly concave above, convex below, soon glabrescent; lamina elliptic to oval or obovate, 2–5.5 (–7.5) cm. long and 1.3–3.5(–4.8) cm. across (leaves of saplings oval to oblong, to 11.2 cm. long and 3.5 cm. across), rounded to bluntly pointed at apex, rounded to cuneate or subtruncate at base, soon glabrescent apart from a few subpersistent small brown hairs on the midrib below, coriaceous, drying greenish brown to brown above and below, margin slightly recurved, hardly undulate, midrib above gradually narrowed from the base, flat to somewhat depressed, 0.3–1 mm. across at the midpoint, becoming slightly raised near the top, raised below, ± angled in the top part, substriate near the base, venation subobscure above, prominulous below, slightly raised, 8–15 veins/5 mm., angle of divergence ca. 60°. Inflorescences from foliate axils, very rarely terminal, 5–11-flowered; axis 0.5–7.5 cm. long, glabrous or almost so, basal internode (0.3–)1–2.5 cm. long, unbranched; bracts often foliaceous, ovate to obovate, 1.5–10 mm. long, caducous to subpersistent; pedicels 4–17 mm. long, glabrous. Flowers hermaphroditic; tepals 8–12, glabrous or fringed with short hairs, outer two suborbicular to elliptic, 4.5–6 mm. long and 4–5.5 mm. across, next two (when more than 8) ca. 5.5 mm. long and 3.5–4.3 mm. across, inner tepals ± elliptic, 7–9.5 mm. long and 2.5–5 mm. across; stamens 85–255(–320), filaments to 3.5 mm. long, connate for up to 0.6 mm., anthers suboblong, 0.6–1.3 mm. long, apex rounded to retuse; ovary 1.3–2.5 mm. long, glabrous; style 2–3.5 mm. long; stigma peltate, 0.7–1.3 mm. across, 1–3-radiate. Fruit ellipsoid, ca. 2.5 cm. long and 1.2 cm. across, ± beaked, beak to 7 mm. long, sharply pointed, drying smooth, brown; outer layer ca. 0.4 mm. across, compact; stony layer absent; spongy layer absent; seed ca. 1.5 cm. long and 1 cm. across.

ADDITIONAL SPECIMENS SEEN. **Mauritius:** Bel Ombre, near S.W. coast, ca. 240 m., *Coode 4057* with *Julien & Guého* (A, K), ca. 240 m., *Coode 4059* with *Julien & Guého* (A, K), ca. 250 m., *Coode s.n.* 14 Nov. 1973 (K); vers Cascade Alexandra, *Friedmann 2667* (K); Alexandra Falls, ca. 650 m., *Coode 4678* (K); Plaine Champagne, 660 m., *Coode 4450B* with *Guého & Lorence* (A, K),

660 m., *Coode 4452* with *Guého & Lorence* (A, K), *Friedmann 1177* (P); Plaine Champagne road, near turning to Mt. Cocotte path, *MAU 12521* coll. *Lalouette* (MAU); Crown Lands Combo, *Coode 4105* coll. *Forestry Dept.* (A, K); Pétrin, 655 m., *MAU 16671* coll. *Vaughan* (MAU); Crown Land Florin on Mare Longue Plateau, *MAU 15475* coll. *Guého* (K, MAU); Black River gorges, *MAU 16757* coll. *Lorence* (MAU); Montagne Blanche, *Bouton s.n.* (K, *pro parte*); Kanaka, Curepipe, *MAU 101* coll. *Bijoux* (MAU), *MAU 104* coll. *Lanémillante* (MAU); *sine loco*, *Horne s.n.* (K), *Franco-British Exhibition* (K); *ibid.* (uplands or hill forest), *MAU 98, 99, 100, 102, 103, 197, 16670* (all MAU).

FIELD CHARACTERS. Outer bark yellow when young, becoming pink and gray with vertical pustular lenticellar lines, finally becoming fissured; under surface bright orange-brown to deep brown; under bark salmon to dark red-brown; inner bark paler pinkish brown. Latex yellow, clear. Young leaves yellowish in color.

ECOLOGY. *Calophyllum parviflorum* is common in colline forests and shrubbery, sometimes rather exposed, and has been found at altitudes of 240 to 660 meters. Specimens in flower have been collected in February, March, and from July to September; a specimen in fruit was found in December.

LOCAL NAME. "Tatamaka à petites feuilles."

Calophyllum parviflorum is characterized by its rather small leaves, which have a broad sunken midrib on the upper surface, and by its beaked and/or sharply pointed fruits, which have a thin, compact, outer layer and entirely lack a woody layer, at least when mature (see below).

There are four shoots on two sheets in the type folder of *C. parviflorum* at Kew; none of the four elements are annotated by Baker. The flowering specimen from Justice Blackburn's herbarium is selected as the type. It agrees fairly well with Baker's description of the leaves ("2–3 in. long, very rigid, obovate with a cuneate base and very short petiole"), and its flowers have eight tepals; Baker describes the flower as having four petals. On the same sheet is a specimen collected by Horne, on which Baker seems to have based his description of the fruit ("oblong, ¾ in. long, with a very distinct beak"). The specimen from Blackburn's herbarium agrees fairly well in foliar characters with the other specimens cited here; that collected by Horne agrees less well, having very rigid leaves (but cf. Baker's description). My description of the fruits of *C. parviflorum* is based on Horne's specimen, but young fruits of specimens more typical in foliar characters are also sharply pointed and are probably of the same type (see below).

On the other sheet the two elements have but a single label and were collected by M. Bouton. On the label is written "vulgo: Tatamaka petite feuille à limbes," perhaps the source of Baker's local name, "Tatamaka à petites feuilles." However, neither specimen is selected as the type, since both have rather large flowers, usually with more than eight tepals. One specimen, belonging to *C. eputamen*, has leaves up to 9 cm. (some-

what over 3 in.) long; the other, perhaps to be referred to *C. spectabile* sensu stricto, has very clearly petiolate leaves.

The specimens cited agree well with each other, differences in the persistence of the foliaceous bracts being unimportant. *Friedmann 2667* has terminal inflorescences, but it is otherwise unremarkable. Only a single collection (*Horne s.n.*) has ripe fruit, and further collections are much needed to clarify the variation found in the immature fruits. Some collections, e.g., *MAU 100* and *MAU 16757*, have a distinct, albeit very thin, woody layer; the fruits of the latter specimen are up to 3.7 cm. long. *Coode 4678* has ellipsoid fruits only 1.7 cm. long and 7 mm. across, which quite lack a woody layer; the outer layer of the fruit is ca. 1 mm. across and is almost areolate because of the prominent latex canals. In the other specimens with fruits (including *Horne s.n.*), the outer layer is thinner and somewhat fibrous, although there are also prominent latex canals.

Although clearly related to *Calophyllum eputamen*, *C. parviflorum* can usually be easily distinguished from it (see the former species). There are two specimens which are somewhat intermediate. *MAU 15475* has rather large leaves and flowers with very numerous stamens (see the upper limits of the measurements in the description). However, its immature fruits have a very thin outer layer, and its flowers are not very large. *MAU 16670* has a broadly elliptic lamina which is very rigid and dries chestnut brown in color. However, the lamina is not very large, and it is much broader than that of *Horne s.n.*, the only other specimen with a comparably rigid lamina.

Calophyllum parviflorum has been reported from Madagascar (see Perrier de la Bâthie, 1951). However, the specimens on which this report was based have a thick woody layer in the fruit and leaves lacking the broad, sunken midrib of *C. parviflorum*; these specimens represent an undescribed species. *C. tacamahaca*, to which Vesque (*loc. cit.*) reduced *C. parviflorum* (as a variety) because of the similarity in the shape of their fruits, also has a woody layer in the fruit. In addition, it has a lamina which is acute at the apex and which has a less obviously sunken midrib than that of *C. parviflorum*.

4. **Calophyllum soulattri** Burm. f. Fl. Ind. 2: 121. 1768. TYPE: described from Java.

Tree. Terminal bud flattened-conoid, 8–12 mm. long, brown-tomentose; twigs flattened, 3–4.5 mm. across, with 4–6 raised lines, rather quickly becoming rounded, drying rather light brown, tomentose when young (hairs ca. 0.7 mm. long), glabrescent; internodes 2.5–8.5 cm. long. Petiole 1.1–1.6 cm. long, narrowly concave above, convex below, tomentose below, at least when young; lamina ovate to oblong, 11–23 cm. long and 3.2–7.4 cm. across, gradually narrowed to the acute apex, or subacuminate, cuneate to broadly cuneate at base, glabrous apart from a few persistent hairs on the midrib below, subcoriaceous, drying dull greenish brown on

both surfaces, margin undulate, slightly and narrowly recurved, midrib above abruptly narrowed at the base, raised, 0.2–0.35 mm. wide at the midpoint, below prominent, raised, striate, or angled toward the base, venation prominulous above and below, raised, 10–15 veins/5 mm., angle of divergence 65–70°. Inflorescences axillary, 9–17-flowered, axis to 3.6 cm. long, tomentose at the base, otherwise almost glabrous, basal internode 0–2 mm. long, flowers flabellate, branches to 1.7 cm. long, each 5-flowered; bracts unknown; pedicels 1.5–2.6 cm. long, glabrous, slender. Flowers hermaphroditic; tepals 4, abnormally 5, sparsely fringed with short hairs, the two outer broadly ovate, 5.5–6.5 mm. long, the inner tepals subelliptic, 7.5–8 mm. long and 2.5–5.5 mm. across; stamens 55–100, filaments to 3 mm. long, connate at the very base, anthers oblong, 1.3–2.2 mm. long, apex ± retuse; ovary ca. 1.5 mm. long, glabrous; style 2.5–3.5 mm. long; stigma peltate, 1–1.3 mm. across, not obviously lobed. Fruit spherical to broadly ovoid, ca. 11 mm. long and 10 mm. across, sometimes apiculate by the style base, drying brown, ± smooth; outer layer detaching from the stone, 0.8–1.4 mm. across, ± compact, but air spaces developing under the skin, not dense; stone ellipsoid, ca. 8 mm. long and 6.5 mm. across, apiculate, walls ca. 0.4 mm. across, smooth, unmarked; spongy layer thin.

SPECIMENS SEEN. **Mauritius:** Jardin de Maurice, *Richard s.n.* (P); Jardin de Pamplemousses, *Boivin s.n.* (P), *MAU 3040* coll. *Delord* (MAU), *MAU 10748* coll. *Guého* (MAU), *Andersson s.n.* March, 1853 (MAU), *anon.* (K); *sine loco*, *Richard 416* (P, *pro parte*), *Bouton s.n.* (K), *De Montbrison s.n.* (FI). **Réunion:** hauts de Bras-Panon (la Caroline), 200 m., *Cadet 4893* (K).

ECOLOGY. *Calophyllum soulattri* grows in waste places or where the vegetation has been disturbed; it has been found at an altitude of 200 meters. Specimens in flower have been collected in March, a specimen in fruit in October.

LOCAL NAME. "Mangue à grappe" (Réunion).

Calophyllum soulattri is a very distinctive species characterized by its thinly coriaceous lamina, which dries dull greenish brown and has dense, fine venation. The inflorescence, with its short basal internode, relatively long lateral branches, and flabellate flowers, is also distinctive. *C. soulattri* is the only species in the Madagascar/Mascarene area which has flowers with four tepals.

Calophyllum soulattri is possibly naturalized in Mauritius; it is rare outside the Botanic Garden at Pamplemousses (*MAU 10748*). P. Rivals notes on *MAU 3040* that *C. soulattri* is naturalized at Ste. Suzanne on Réunion. *C. soulattri* may also be naturalized on Madagascar, but I have seen only two specimens from there (*Bréon s.n.* (P) and *anon.* (MEL *62306*)), most of the specimens cited under *C. spectabile* (auct. non Willd., = *C. soulattri*) by Perrier de la Bâthie (1951) belonging to other species.

Perrier de la Bâthie (1951) thought that *Calophyllum soulattri* had

been introduced into Madagascar and the Mascarenes from India. *Calophyllum soulattri* is not native in either India or Ceylon, and it was probably introduced from the Malesian region.

5. **Calophyllum tacamahaca** Willd. Sitzungsber. Ges. Naturf. Fr. Berlin Mag. **5**: 79. 1811; Choisy, Mém. Soc. Hist. Nat. Paris 1: 228. 1823; Choisy in DC. Prodr. 1: 562. 1824, *pro parte* Bourbon; Sprengel, Syst. Veg. ed. 16. 2: 571. 1825; Cambess. Mém. Mus. Hist. Nat. Paris **16**: *pl. 17C*. 1828; G. Don, Gen. Syst. 1: 622. 1831, *pro maj. parte*; Bojer, Hort. Maurit. 52. 1837; Wight, Ill. Ind. Bot. 1: 128. 1840; Choisy, Mém. Soc. Phys. Hist. Nat. Genève 12: 423. 1851, *pro parte* Mascarenes; Planchon & Triana, Ann. Sci. Nat. Bot. IV. **15**: 286. 1861; Vesque, Epharmosis 2: *tab. 2*. 1889; Vesque in DC. Monogr. Phanerog. **8**: 547. 1893, *pro parte* Mascarenes; Cordemoy, Fl. Île Réunion 333. 1895. TYPE: Bourbon [Réunion], *du Petit-Thouars s.n.* (holotype, B, *herb. Willd. 10115*).

C. spectabile Willd. Sitzungsber. Ges. Naturf. Fr. Berlin Mag. **5**: 79. 1811; Choisy, Mém. Soc. Hist. Nat. Paris **1**: 228. 1823; Choisy in DC. Prodr. **1**: 562. 1824, *pro parte* Mauritius; Sprengel, Syst. Veg. ed. 16. **2**: 571. 1825; G. Don, Gen. Syst. **1**: 622. 1831, *pro parte*; Bojer, Hort. Maurit. 52. 1837. TYPE: Île de France [Mauritius], *du Petit-Thouars s.n.* (holotype, B, *herb. Willd. 10116*).

C. lanceolatum Bl. Bijd. **4**: 217. 1825; Miq. Fl. Ind. Bat. **1**(2): 511. 1859. TYPE: described from cultivated material originating from Mauritius.

C. lanceolarium Roxb. Fl. Ind. ed. 2. [W. Carey, ed.] **2**: 608. 1832; Roxb. Hort. Bengal. 41. 1814 et G. Don, Gen. Syst. **1**: 623. 1831, *nomina*; Hooker & Arnott, Bot. Beech. Voy. 173. 1833; Wight, Ill. Ind. Bot. **1**: 129. 1840. TYPE: described from cultivated material originating from Mauritius (BM).

C. inophyllum auct. non L.; Lamarck, Encycl. Méth. Bot. **1**: 552. 1785, *pro parte* Mascarenes; Baker, Fl. Maurit. 16. 1877, *pro syn.*

Tree 10–15 m. tall, to 25 cm. d.b.h. Terminal bud plump, 4–8 mm. long, with short furfuraceous gray to brown indumentum; twigs hardly flattened, 1.5–3.5 mm. across, ± 4-angled at first, soon with a variable number of raised lines, young twigs drying brown to dark brown, slightly older twigs grayish brown, glabrous or with sparse brown farinose indumentum when young; internodes 0.5–2.7(–4.5) cm. long. Petiole (0.7–) 1.1–2.5 cm. long, 1.3–3 mm. wide, ± V-shaped above, convex below, glabrous when mature; lamina elliptic, sometimes ovate to suboblong, (6.3–) 8–18.8 cm. long and (2–)3.4–5.5(–6.8) cm. across, ± acute at apex, very rarely subrounded, (broadly) cuneate to acute at base, sometimes narrowly decurrent, glabrous, or rarely with subpersistent brown farinose indumentum on the midrib below, chartaceous to subcoriaceous, usually drying greenish brown above and below, with light brown margins and midrib, ± shiny, rarely dark brown on both surfaces, margin undulate, slightly recurved, midrib above gradually narrowed from the base, de-

pressed, 0.3–1.0 mm. across at the midpoint, becoming raised toward the apex, below raised, ± striate, venation prominulous above and below, raised, (5–)7–12 veins/5 mm., angle of divergence 60–80°. Inflorescences from foliate axils, 7–many-flowered, axis 3–11 cm. long, glabrous or with sparse farinose indumentum on the lowest internode, basal internode (0.2–)0.6–2.6 cm. long, usually unbranched, rarely with 3-flowered branches to 2 cm. long; bracts unknown; pedicels (0.6–)1.3–2.1 cm. long, glabrous or almost so. Flowers hermaphroditic; tepals 7–9, fringed with short hairs, the two outer tepals broadly ovate, 7.5–11 mm. long and 6.5–9.5 mm. across, thick, concave, inner tepals 11–17 mm. long and 4.5–9 mm. across; stamens 200–355, filaments to 7 mm. long, connate for up to 1 mm., anthers oblong, 1.5–1.9 mm. long, apex ± retuse; ovary 2–3 mm. long, glabrous; style 4.5–5 mm. long; stigma peltate, ca. 1.1 mm. across, 3–4-lobed. Fruit ovoid, 3.7–4.3 cm. long and 2–2.3(–3.7) cm. across, ± sharply pointed at apex, drying grayish to light brown, deeply and sharply wrinkled; outer layer 2.5–4 mm. thick, compact and rather hard; stone ovoid to ellipsoid, 1.8–2.6(–3.1) cm. long and 1.4–2.1(–2.5) cm. across, pointed at apex, wall 0.9–1.5 mm. thick, smooth and unmarked, with a plug 4(–8?) mm. across; spongy layer rather prominent(?), up to 1 mm. thick.

ADDITIONAL SPECIMENS SEEN. **Mauritius:** Deux Mamelles near Pieter Both, 510 m., *Coode 4361* with *Guého & Lorence* (somewhat similar to *C. parviflorum*; A, K); Montagne Blanche, etc. *Bouton s.n.* (K, *pro parte*); Bel Ombre, ca. 250 m., *Coode s.n.* 14 Nov. 1973 (fragmentary collection, A, K); Mt. Saint Pierre, *Barclay 1711* (K); Plaine Lièvre, near road to Brise Fer, *MAU 14546* coll. *Edgerley* (MAU); Crown Land Dangnell, near Port Louis, ca. 60 m., *MAU V/3160* coll. *Vaughan* (MAU); Crown Land Vuilliman, near "Piton de Milieu," *MAU 1385* coll. *Vaughan* (MAU), *MAU 16668* coll. *Edgerley* (MAU); Crown Land Cabinet, *MAU 57* coll. *Duljeet* (MAU); halfway down new Cabinet Maggenta Road, 240 m., *MAU 65* coll. *Duljeet* (MAU); near Crown Land Rivière, Tamarin Falls, *MAU 16669* coll. *Vaughan* (MAU); in sylvis vastis, *Bojer s.n.* (K); *sine loco*, *Sieber Fl. Maurit. 2, 110* (B, BM, K, P), *S[ieber] Fl. Mixta 116* (E), *Commerson 149* (P), *Commerson s.n.* (BM, C, P, P–JU *11883*), *Bouton s.n.* (K, *pro parte*), *Hornemann s.n.* (C), *MAU 1645, 2851, 3032* (all MAU). **Réunion:** Mare Longue, near St. Philippe, 500–600 m., *Coode 4174* with *Cadet & Badré* (A, K), 500–600 m., *Coode 4175* with *Cadet & Badré* (A, K), *28175 SF* coll. *Capuron* (P), *Maillot & Jules 3* (P), 100 m., *Cadet 3793* (REU), 400 m., *Cadet 3844bis* (REU); route de Tacamaca, 500 m., *Friedmann 1548* (P); la Montagne, 600 m., *Cadet 613* (REU); Tremblet, near sea level, *Coode 4966* with *Cadet* (K), St. Philippe, *Cadet 563* (REU); hauts de Bras-Panon (la Caroline), 400 m., *Cadet 4812* (REU); route National entre Basse Vallée et Vincendo (St. Philippe), 100 m., *Cadet 3521* (K); Passim, *Cordemoy s.n.* (P); *sine loco*, *Cordemoy s.n.* (P), *Commerson s.n.* (P, P–JU *11881*), *Labillardière s.n.* (FI, *pro parte*). **Mascarenes(?):** *sine loco*, *herb. Schumacher*, comm. *Jussieu* (C).

FIELD CHARACTERS. Outer bark smooth, yellowish or gray in patches, brown on the under surface; under bark brownish red; inner bark pink, paler toward the cambium. Latex yellow, clear, that from cut leaves white. (Details from *Coode 4174*.)

Ecology. *Calophyllum tacamahaca* usually grows in colline habitats, sometimes on rocks (e.g., *Barclay 1711*, from Mauritius) or on recent lava flows (e.g., *Maillot & Jules 3*, from Réunion); it has been collected at altitudes of (0–)100 to 600(–900) meters. It may grow in drier places than *C. eputamen* and *C. paviflorum*, although on Réunion it occurs in the wettest place in the lowlands, which is wetter than anywhere on Mauritius (Coode, pers. comm.). It has several times been collected from disturbed or secondary vegetation. Flowering specimens have been collected in February and March, and flowering is reported in April and May as well by Bojer (*loc. cit.*); fruiting specimens have been collected in May, October, and November. According to the field notes on *Maillot & Jules 3*, the fruits have the taste of apricots.

Coode 4174 has galled leaves; the galls are pustular outgrowths of the lamina, sometimes completely deforming it.

Germination. The radical emerges just to one side of the basal plug, the stone where it emerges being about half the thickness of the rest of the wall. The basal plug is pushed out, and the area of thin stone lost during germination is of similar size and shape to that of the basal plug and may also be delimited by a line of weakness. Three, four, or five pairs of seedling leaves are produced, each pair separated by internodes (0.5–)1–4 cm. long. The lowest pair of leaves, which is probably sometimes reduced, had been lost in two of the five seedlings seen. The seedling has a prominently 4-angled stem. (Details from *Coode 4175* and *MAU 2851.*)

Local names and uses. "Tatamaca," "tatamaca rouge," "tatamaca des hauts." *Calophyllum tacamahaca* is a useful timber species.

Calophyllum tacamahaca is probably related to *C. inophyllum*, from which it can be separated by its relatively longer terminal bud and narrower twigs with shorter internodes, by its more narrowly elliptic or ovate lamina with an acute apex and a midrib narrowing only gradually from the base, and by its shorter pedicels, pointed fruits, etc. (see Table 1). The fruits of both species dry sharply wrinkled and pale in color, and the method of germination described above for *C. tacamahaca* is very similar to that described for *C. inophyllum* (Stevens, 1974). Planchon and Triana (*loc. cit.*) discuss the early history of the confusion between the two species. It has been suggested that *C. tacamahaca* is no more than a variety of *C. inophyllum* (Baker, *loc. cit.*; Vesque, *loc. cit.* 1893; Perrier de la Bâthie, 1951), but the differences noted above readily separate the two.

Numerous fruiting collections of *Calophyllum inophyllum* from all over its range have been examined, and in nearly all the stone is spherical and rounded at the apex (and base), although the fruits themselves may have a stipe over 1 cm. long or be prominently pointed at the apex. A few collections have slightly elongated stones, but the apex is rounded; only one collection examined, *bb 29896* (Forest Research Institute, Buitenzorg), from the Moluccas, had an apiculate stone. The somewhat

unfortunately named *C. inophyllum* var. *takamaka* Fosberg, from Aldabra, agrees with typical *C. inophyllum* in all the respects discussed above. *Calophyllum inophyllum* characteristically has a plug at the base of the stone.

Calophyllum tacamahaca is also closely related to *C. recedens* Jumelle & H. Perr., from Madagascar. That species has more slender twigs, leaves which have rather denser venation and which are acuminate at the apex and often attenuate/decurrent at the base, narrow tepals, and smaller fruits with stones less than 0.7 mm. thick (TABLE 1). As these are not great differences, further studies are needed to establish the rank of *C. recedens*.

TABLE 1. **Comparison of Calophyllum inophyllum with C. tacamahaca and C. recedens.**

	C. inophyllum	C. tacamahaca	C. recedens
Color of older twigs when dry	mid-brown	grayish brown	mid-brown
Twig width (mm.)	3–5.5	1.5–3.5	1.5–2.8
Lamina apex	rounded	± acute (–sub-rounded)	acuminate
Midrib on upper surface — width at midpoint (mm.)	0.4–0.8	0.3–1	0.2–0.35
Venation density (veins/5 mm.)	5–8(–10)	(5–)7–12	8–18
Lowest internode of inflorescence (cm.)	0.2–0.5(–0.9)	(0.2–)0.6–2.6	0.7–1.7
Pedicel length (cm.)	1.5–5	(0.6–)1.3–2.1	0.7–2
Fruit shape	spherical to ellipsoid	ovoid	ovoid to ellipsoid
Thickness of outer layer (mm.)	1.9–2.3	2.5–4	1.6–2.5
Apex of stone	rounded	obtusely pointed	rounded to mucronate
Stone thickness (mm.)	ca. 1	0.9–1.5	0.3–0.6

The synonymy given above for *Calophyllum tacamahaca* is not definite. The type specimen of *C. tacamahaca*, collected on Réunion, has narrow petioles and a rather small, rigid lamina which has dried a greenish brown. It represents the common form of the species. The type of *C. spectabile* (from Mauritius) has rather thinner, larger leaves which have dried a dark brown, and it is similar in this respect to *Maillot & Jules 3*, from Réunion. Other dark-drying specimens are more like typical specimens of *C. tacamahaca*. The equation of *C. spectabile* with *C. soulattri* Burm. f. would appear to stem from Willdenow's suggestion that Rumphius's *Bintangor sylvestris* (= *C. soulattri*) was the same as *C. spectabile*; this has been discussed on p. 182.

The original description of *Calophyllum lanceolatum* Bl. reads "ramulis 4-aèdris, foliis oblongo-lanceolatis obtusis basi acutis." It was based on material grown at Buitenzorg which originated from Mauritius, and it seems to represent a specimen similar to that on which *C. lanceolarium* Roxb. was based.

There is a specimen of *Calophyllum lanceolarium* Roxb. at BM which is probably a type. On one sheet is written "*C. lanceolaria*" and "1811," with "x 19" below the 1811, and on another sheet is written "(illegible) Jannet." Roxburgh (*loc. cit.* 1814) refers to Monsieur Jannet (see the discussion under *C. inophyllum* above) as having sent this species to Calcutta in 1810. The specimen at BM agrees with the description of *C. lanceolarium*; it is possibly a sapling of *C. tacamahaca*, having short, branched hairs on the terminal bud like those of that species. Two specimens from Réunion, *Cadet 613* and *Cadet 4812*, have especially prominently angled stems; both were collected from small individuals (*Cadet 613* — "arbuste de sous-bois"; *Cadet 4812* — "un rejet"). The seedlings of *C. tacamahaca* also have prominently angled stems. Although the specimen of *C. lanceolarium* at BM also looks like *C. apetalum* Willd., an Indian species, the hairs on the terminal bud seem to be only rarely branched in the latter species.

Most of the specimens assigned to *Calophyllum tacamahaca* from both Mauritius and Réunion are similar and match the type of *C. tacamahaca*. However, specimens with broader petioles are common on Réunion but very rare on Mauritius. Similar fruits are associated with specimens matching the types of both *C. tacamahaca* and *C. spectabile*, as well as with the broad-petioled specimens from Réunion.

Fruits preserved in formalin have been seen (*Cadet 3793* and *Cadet 3844bis*). (Leaves associated with these specimens have not been seen.) Although the fruits of *Cadet 3844bis* are immature, in both specimens the stones are acute at the apex. The fruits of *Cadet 3793* are ovoid, ca. 4.3 cm. long and 3.7 cm. across, and the surface is smooth. The outer layer is ca. 5 mm. thick, and the stone, which is ca. 3.1 cm. long, 2.5 cm. across, and slightly larger than those of the other specimens seen (cf. the description), has walls 1.3–1.5 mm. thick.

MAU 14546 has fruits similar to those characteristic of the species. Although they are less deeply wrinkled (owing to their immaturity), they have a prominent woody layer. However, the leaves are more coriaceous, the apex of the lamina is subrounded, the midrib is prominent, and the petiole is broad; as a result, the specimen approaches *C. eputamen* in appearance.

The Identity of Calophyllum acuminatum

Calophyllum acuminatum Lamarck, Encycl. Méth. Bot. 1: 553. 1785.

The description of this species reads "CALOPHYLLUM acuminé, *Calophyllum acuminatum. Calophyllum foliis ovato-oblongis, acutis, fructibus*

ovatis acuminatis. N. *Bintangor sylvestris*. Rumph. Amb. 2. p. 216. Tab. 72?" This description was based on dried material, as the mention "*v. s. en fr.*" at the end of the protologue confirms.

The specimen of *Calophyllum acuminatum* in Lamarck's herbarium at Paris contains two elements, a leafy shoot of a species of *Garcinia* and a fruit of a species of *Calophyllum* cut longitudinally. Lamarck's discussion makes it probable that these are the elements on which he based his *C. acuminatum*. He mentions the dull leaves of *C. acuminatum* with "nervures moins fines" (hence with more distance between the veins) than in those of *C. inophyllum* and *C. calaba*. His interpretation of these two latter species was unusual, but in his herbarium there is material of both of these as they are currently interpreted. There is also material to be referred to *C. tacamahaca*, which he included in his concept of *C. inophyllum*. The leaves of the shoot of *Garcinia* are dull, with venation more distant than that of the species of *Calophyllum* mentioned (as might be expected of a species of *Garcinia*). The fruit on the sheet is sharply pointed at the apex and has a prominent and hard woody layer, agreeing well with Lamarck's statement "ses fruits sont des noix ovales et acuminées."

Calophyllum acuminatum, when it has been mentioned at all, has generally been included in the synonymy of *C. soulattri* Burm. f. or of *C. spectabile* auct. non Willd. The reason for this seems to be Lamarck's mention of Rumphius's *Bintangor sylvestris* after his description of *C. acuminatum*; Willdenow made a similar hesitant reference to *Bintangor sylvestris* in his description of *C. spectabile*, where he also equated *C. spectabile* with *C. acuminatum* ("scheint Lamarck's *C. acuminatum* dieselbe Pfanze zu sein"), so again leading back to *Bintangor sylvestris*. Choisy also thought that the three species of *Calophyllum* might be the same (see, for example, 1824). Hasskarl (Abh. Naturf. Ges. Halle 9: 184. 1866), in his interpretation of Rumphius's names, equated *Bintangor sylvestris* with *C. acuminatum*, *C. soulattri* and *C. spectabile* being synonyms. However, the fruits of *Bintangor sylvestris* (*C. soulattri* Burm. f.) are often subspherical and dry dark in color; the stone is thin, usually less than 0.4 mm. thick. Planchon and Triana (1861) inadvertently omitted any mention of *C. acuminatum* Lamarck, although they did include a later homonym, *C. acuminatum* Willd., which is a species of *Rheedia*. Vesque (1893), the last monographer of *Calophyllum*, also made no mention of *C. acuminatum* Lamarck. Another result of all this confusion was that the name *C. spectabile* was used fairly generally until about 1950 for the taxon properly called *C. soulattri*; not only are the two names not synonymous, but *C. soulattri*, the earlier name, was often cited as a synonym of *C. spectabile*.

Since Lamarck distinguished *Calophyllum acuminatum* from other species of the genus on vegetative characters which were taken from the shoot of *Garcinia*, it is proposed that *C. acuminatum* be typified by the leafy shoot. The epithet "*acuminata*" is already occupied in *Garcinia* (*G. acuminata* Planchon & Triana), and my knowledge of this difficult genus is too poor to suggest to which species the leafy element of *C. acuminatum*

might belong. *Calophyllum acuminatum* was supposed to come from Java and the Moluccas, and if Lamarck was correct in this and not confused by his reference to Rumphius, the leafy shoot may come from this region (see below).

The fruit of *Calophyllum acuminatum*, with its sharply pointed apex, seems to have suggested Lamarck's specific epithet. The fruit probably comes from what is properly called *C. tacamahaca*, a Mascarene species(!). However, the fruiting element of *C. acuminatum* does not seem to have been the main element in Lamarck's separation of his species, so typification on this element would be unsatisfactory.

Additional Species Recorded

Calophyllum calaba L. Sp. Pl. 514. 1753; Bojer, Hort. Maurit. 52. 1837.

Bojer (*loc. cit.*) reported that *Calophyllum calaba* was cultivated at the Jardin du Roi and at Reduit, but I have not seen any material from either Madagascar or the Mascarenes referable to this species. The name *C. calaba* was much confused in the early years of the nineteenth century. The name is correctly applied to a species common in the Caribbean, in Central America, and in parts of South America. This species is characterized by its elliptic to suboblong lamina, which is usually rounded at the apex, and by its shortly pedicelled, rather small flowers with relatively very large anthers. *Calophyllum calaba* has been grown in both India and Ceylon, and Bojer (*loc. cit.*) gave the place of origin as the Antilles, so it is possible that it once was grown on Mauritius. The name *C. calaba* has also been used for *C. inophyllum* and two species now called *C. apetalum* Willd. (from India) and *C. burmannii* Wight (from Ceylon).

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THE SEEDS OF THE MONSTEREAE: THEIR MORPHOLOGY AND FOSSIL RECORD

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THE TRIBE MONSTEREAE of the family Araceae includes some of the most magnificent and characteristic of tropical lianas. The subdivision of the tribe into genera, based largely on the placentation and septation of the ovary, has been disputed for more than a hundred years, and recent treatments indicate a continuing lack of consensus (e.g., Bakhuizen van den Brink, 1958; Bunting, 1962; and Hotta, 1970). The present paper reports the results of a study of seed morphology initiated to clarify the generic limits in this group and to account for a number of fossil seeds ascribed to one of the included genera.

Taxonomists working on the Monstereae in the past have neglected seed morphology, except for Engler and Krause (1908), who used the presence or absence of endosperm as a generic character. However, it is apparent from various erroneous illustrations that they often did not correctly interpret other features of the monsteroid seed, in particular the path of the vascular bundle in the funiculus and raphe. Our preliminary survey indicates that seed morphology is taxonomically useful at the generic or specific level in the Monstereae as well as in other tribes of the Araceae.

MATERIALS AND METHODS

This study is based primarily on specimens of about 70 species in the herbaria of the Arnold Arboretum (A) and the Gray Herbarium (GH) of Harvard University; additional reports in the literature bring the total number of species investigated to about 80. This number is approximate, because the tribe is sorely in need of revision and the specific identification of specimens is often doubtful. Developmental studies in *Rhodospatha* and *Monstera* are based on material collected in the wild and preserved in formalin-acetic-alcohol (voucher specimens in GH). Developmental studies in other genera are based on rehydrated herbarium material. Published illustrations of the fossils have been examined, but not the fossils themselves.

MODERN SEEDS

In the seeds of the Monstereae there is a correlation between size, curvature, and relative abundance of endosperm. The range includes small uncurved seeds with relatively abundant endosperm to large highly curved seeds lacking endosperm. In this series six morphologically distinct types

of seeds may be recognized. Each genus accepted by Engler and Krause (1908) is constant for one of these types, but their genera are not all separable by this character alone.

Seeds of a number of extant species are illustrated in FIGURES 1 to 47; the letters c, h, m, and r in FIGURES 1 to 6 refer respectively to the chalaza, hilum, micropyle, and raphe. The term "ventral face" is here applied to the side of the seed bearing the raphe, which faces the placenta or the axis, while the "dorsal face" is directed either upward or outward.

Stenospermation Schott (FIGURES 1, 8, 9) is a neotropical genus of about 20 species characterized by smooth, anatropous, subterete seeds 2–2.5 mm. long and 1 mm. in diameter. The seeds are flattened on the ventral (raphal) surface and slightly dorsally inflated toward the chalazal end. The adnate funiculus forms a ventral raphe visible as a dark line leading to the chalazal end; the micropyle is dorsal to the hilum on the flattened nucellar end. In the development of the seed the anatropous ovule elongates but does not become curved. The embryo is straight and fusiform, surrounded by abundant endosperm.

Rhaphidophora Hassk. (FIGURES 2, 10–20) includes about 60 species occurring in West Africa, from Indomalesia to Samoa, and north to Formosa. The seeds are smooth, anatropous, subterete to ellipsoid, 1–3 mm. long, and 0.5–1 mm. thick. The subterete specimens have a flattened raphe-bearing ventral face similar to that of *Stenospermation*. In the ellipsoidal forms (FIGURES 10, 14, 17), the ventral face is not flattened. In general the seeds of *Rhaphidophora* are very similar to those of *Stenospermation*. In both of these genera the small size of the seeds is clearly related to the large number of seeds per ovary, but even in those specimens which set only a few seeds per fruit, the size and morphology of the seeds remain characteristic of the genus.

Epipremnum Schott (FIGURES 3, 21–25) includes about 15 species ranging from Indomalesia to Samoa and the Marshall Islands. The seeds are symmetrically to asymmetrically reniform, 3–7 mm. long, and 1.5–4 mm. across. The raphe passes from the hilum to the slightly inflated chalazal end along the concave ventral surface, often producing a chalazal ostiole where it penetrates the testa. The micropyle, occasionally represented by a small black hole (as in FIGURE 3), is situated on the inner margin of the nucellar end dorsal to the hilum. The surface morphology varies from smooth (FIGURES 22, 24) to rugose (FIGURES 21, 25). In *E. pinnatum* (FIGURE 23) the surface often but not always bears pits in the hard seed coat; these and the epidermal cells of the testa are arranged in parallel rows following the curvature of the seed axis. The curved embryo is embedded in endosperm.

Rhodospatha Poepp. & Endl. (FIGURES 4, 26, 27) comprises about 15 species of the neotropical mainland. The seeds are anatropous, reni-

form to cordiform in outline and terete to slightly flattened in cross section, 1–1.5 mm. wide, and about 0.5 mm. thick. The fine black raphe passes from the narrowed and occasionally stalklike hilar end along the strongly concave ventral face to the slightly inflated chalazal end (FIGURE 27); the chalaza appears as a black spot in specimens divested of their outer testal layer. The micropyle is dorsal to the hilum on the nucellar end. The dorsal margin of the seed is cristate, and in material preserved in FAA it exhibits radiating processes extending 1–2 mm. beyond the seed surface. During development of the seed, the ovule bends about the raphe, giving rise to the curved condition of the mature seed.

Scindapsus Schott (FIGURES 5, 28–34) includes about 25 species ranging from India and Sikkim to the Solomon Islands and one species in South America. The anatropous seeds, 3–9 mm. long and 2–5 mm. wide, vary in outline from broadly reniform (FIGURES 20, 30) to cordiform, with those of *S. officinalis* almost horseshoe-shaped, the enclosed ventrally directed space being covered by a membrane (FIGURE 31). In cross section the seeds are round to ellipsoidal. The raphe passes along the concave ventral surface from the hilum to the chalazal end, which in some species (FIGURES 28, 30, 32) is longer than the nucellar end. In *S. officinalis* (FIGURES 5, 31) the hilum is marked by an irregularly bordered scar which overlies the chalazal end. The micropyle is dorsal to the hilum and is subtended dorsally by a thickened ridge. The outer surface is smooth (FIGURES 30, 32, 33) or faintly radially striate (FIGURES 28, 29, 31, 34). The developing seed is initially straight, but it curves around the raphe as it grows. The embryo is macropodial and endosperm is lacking.

Monstera Adanson (FIGURES 6, 7, 35–44), a neotropical genus of about 25 species, has oblong-ellipsoidal to subglobose seeds 6–18 mm. long and 4–12 mm. wide. The morphology of these seeds is best understood by considering their ontogeny, as illustrated by *M. dubia* (FIGURE 7). The developing anatropous ovule is initially only slightly curved, but in growth it reflexes about the funiculus, thereby causing the raphe to follow an S-shaped course in the mature seed. The hilum appears either as a small stalk (FIGURES 6, 7, 42) or as a depressed channel (FIGURES 35, 37–40, 43, 44). The micropyle is on the opposite side of the hilum from the chalaza. The ontogeny of the seeds of most species is culminated by growth in the dorsal direction, yielding a dorsoventrally elongate shape. The smooth surface of the seed is frequently marked by numerous light-colored raphide sacs embedded in the soft testa. The embryo is macropodial and endosperm is absent.

Amydrium Schott (FIGURE 45) comprises four species of Thailand and Malesia. In *A. magnificum* the seeds are subglobose to subreniform in outline and approximately 7 mm. long by 9 mm. wide. In the ovule the raphe curves well around the chalazal end, and with later growth

both the chalazal and nucellar ends enlarge considerably and bend ventrally. In the mature seed the funiculus has become adnate to the testa about one third of the way from the nucellar end, and the raphe arches away from the seed above the ventral concavity before entering the chalaza. The seed coat is smooth and is marked by light-colored raphide sacs. The embryo is macropodial and endosperm is lacking. Nicolson (1968) considered this genus to be close to *Epipremnum*, but the limited material at our disposal suggests that its seed morphology is closer to that of *Monstera*. In *Amydrium*, however, most of the seed elongation is lateral rather than dorsal, with the consequence that the raphe is shallowly instead of sharply S-shaped.

FOSSIL SEEDS

Tertiary carpological remains attributed to the Monstereae include three genera and twelve species of seeds and spadices. These range in age from the lower Eocene to the Pliocene and geographically from western Europe through Central Asia, with one specimen reported from the southeastern United States. Comparison of these fossils with modern forms suggests that only four species are assignable to the Monstereae. One fossil may be referred to *Anadendrum* of the subfamily Pothoideae, three more are assignable to the subfamily Lasioideae, and the remaining species are of uncertain affinity. The necessity of comparing published illustrations of these fossils with the modern seeds constrains us to suggest affinities rather than to propose a formal taxonomic revision of the fossil material, although such a revision seems appropriate in many cases. This cautious attitude is reinforced by the possibility of unrecognized similar seed morphologies in groups unrelated to the Araceae. Kirchheimer (1957) has noted the similarity of seeds of *Epipremnum* to those of species of the Leguminosae and Malvaceae.

The identification of the fossils is based on their morphological similarity to modern forms and on the climatic affinities of the floras associated with the fossils. The extant Monstereae are primarily tropical. The association of a putative fossil *Epipremnum* with a pronouncedly temperate flora, particularly when coupled with an inappropriate morphology, suggests the rejection of such a form from the Monstereae. In several cases individual citations within a species are questioned without implying the potential rejection of that species.

SPECIES ASSIGNABLE TO THE MONSTEREAE

Epipremnum crassum C. & E. M. Reid, Pliocene floras of the Dutch-Prussian border. 71. *pl. 4, figs. 1–9*. 1915. [Pleistocene].

DOROFEEV, P. I., Voprosy Geol. Vost. Okr. Russk. Platf. Yuzhn. Urala 5, Bashk. Fil. Akad. Nauk SSSR. 18. *pl. 3, figs. 3, 4*. 1960. [Pliocene]; Dokl. Akad. Nauk SSSR. **144**: 650. *pl. 1, figs. 14, 15*. 1962. [Miocene]; Problemy

Botaniki **6:** 50. *pl. 2, fig. 3.* 1962. [Miocene?]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Western Siberia.] Izdat. Akad. Nauk SSSR. 133. *pl. 16, figs. 13–16.* 1963. [Miocene?]; Bot. Zhur. **51:** 1481. 1966. [Miocene]; Miotsenovaya flora Mamontovoi Gary Na Aldane. [The Miocene flora of the Mammoth Mountain on the Aldan River.] Akad. Nauk SSSR., Bot. Inst. V. L. Komarova. 57. *text fig. 12; pl. 8, figs. 1–5.* 1969. [Miocene]; Tretichnye flory Basseina r. Omoloya. [Tertiary flora from Basseina on the River Omoloya.] Akad. Nauk SSSR. Vsesoyuznoe Botanicheskoe Obshchestvo. 82. *pl. 8, figs. 7, 8.* 1972. [Tertiary].

NIKITIN, P. A., Compt. Rend. Acad. Sci. URSS **3:** 134. 1935. [Miocene–Pliocene]; The Pliocene and Quaternary floras of the Voronezh region. Izdat. Akad. Nauk SSSR. 123. *pl. 3, figs. 33–37.* 1957. [Pliocene].

REID, E. M., Bull. Soc. Géol. France IV. **20:** 63. *pl. 3, figs. 13, 15.* 1920. [Pliocene]; *Ibid.* **23:** 315. 1923. [Pliocene].

VLERK, I. M. VAN DER, & F. FLORSCHÜTZ, Nederland in het Ijstijdvak. 76. *fig. 20.* 1950. [Pleistocene].

Anatropous seed, about 3 mm. long and 2.5 mm. wide, reniform, reflexed approximately 120°–180°; chalazal and nucellar ends of equal length, both rounded, the ventral hollow frequently covered so that the ventral face appears almost flat (with the exception of that figured by Dorofeev, 1969), the ventral face occasionally with a conspicuous round protuberance; surface of the seed smooth to faintly pitted, perhaps from raphide sacs.

The specimens of the fossil are morphologically similar to *Epipremnum*, but they exhibit considerable variability, suggesting that the concept of the fossil may encompass more than one species. In addition, the associated floras range from marginally subtropical to interglacial, suggesting that some of the citations may not refer to seeds of Monstereae. The type specimen and the specimens described by Dorofeev (1962b, 1963) possess a small but prominent ventral protuberance, a feature not seen in any other fossil or modern Monstereae. However, Dorofeev (1963) illustrated four seeds which apparently intergrade from forms possessing this protuberance (FIGURE 16) to those lacking it (FIGURE 14). The significance of this character remains unclear. Dorofeev (1969) illustrated in his *text fig. 12* four forms, of which the one on the lower left is possibly an aroid seed. The remaining three, as well as those illustrated by Dorofeev (1960, *fig. 4*) and Van der Vlerk and Florschütz (1951), are distinct from any monsteroid or lasioid seed seen by us in their deeply rounded shape and often flat, multiperforated ventral face and should be excluded from the Araceae. The morphology of the remaining seeds attributed to this species is best illustrated by Dorofeev (1962a) but is too indistinct to permit certain referral to an extant species. These seeds are most probably allied with the modern genera *Epipremnum* and *Scindapsus*.

It is doubtful that *Epipremnum* could survive the rigors of a European glacial period by migrating over the Alpine system, and the speci-

mens described by Reid and Reid (1915) and Van der Vlerk and Florschütz (1951), already considered dubious on morphological grounds, are of interglacial age. Dorofeev (1960) and Nikitin (1957) described *E. crassum* from deposits particularly poor in thermophilic East Asian elements, suggesting that these specimens, although morphologically acceptable, are also suspect. The remaining floras, although not tropical, are warm-temperate to marginally subtropical and are conceivably capable of supporting *Epipremnum*.

Epipremnum ornatum E. M. Reid & M. E. J. Chandler, The Bembridge flora. Brit. Mus. Nat. Hist. 83. *pl. 4, figs. 24, 25.* 1926. [Oligocene].

Epipremnum ornatum Reid & Chandler.

DOROFEEV, P. I., Dokl. Akad. Nauk SSSR. **101:** 941. *pl. 1, figs. 5, 6.* 1955. [Tertiary]; Sbornik Pamya. A. N. Krystofovich, Akad. Nauk SSSR. Bot. Inst. V. L. Komarova. 301. *tab. 2, figs. 17–19.* 1957. [Tertiary]; Dokl. Akad. Nauk SSSR. **123:** 173. 1958. [Oligocene]; *Ibid.* **123:** 543. 1958. [Oligocene]; *Ibid.* **127:** 1104. 1959. [Oligocene]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Western Siberia.] Izdat. Akad. Nauk SSSR. 131. *pl. 16, figs. 17–21.* 1963. [Tertiary]; Bot. Zhur. **51:** 1481. *pl. 1, fig. 42.* 1966. [Miocene]; Tretichnye flory Basseina r. Omoloya. [Tertiary flora from Basseina on the River Omoloya.] Akad. Nauk SSSR., Vsesoyuznoe Botanicheskoe Obshchestvo. *pl. 8, fig. 9.* 1972. [Tertiary].

KOLESNIKOVA, T. D., Bot. Zhur. **45:** 118. *pl. 1, fig. 2.* 1960. [Miocene]; *Ibid.* **46:** 126. *pl. 1, fig. 4.* 1961. [Miocene].

NIKITIN, P. I., Akvitanskaya Semennaya flora Lagernogo Sada (Tomsk). Izdat. Tomskogo Universiteta. 63. *pl. 7, figs. 5–9.* 1965. [Tertiary].

Rhaphidophora ornata (Reid & Chandler) Chandler, Bull. Brit. Mus. Nat. Hist. Geol. **6**(3): 364. 1963. [Oligocene].

Anatropous seed, 2–3 mm. long, approximately 2.2 mm. wide, reniform, reflexed 90°–160°; tapered nucellar end truncate and in lateral view longer than the rounded chalazal end; seed surface smooth.

These small, smooth seeds appear in both size and shape to belong to one species, although the illustrated type (Reid & Chandler, 1926) is a particularly poor specimen. The morphology and the frequent presence of small pits (perhaps indicative of raphide sacs) place this form, in our opinion, close to the extant species *Epipremnum pinnatum* of southeastern Asia and Oceania. Chandler (1963) places these fossils in the genus *Rhaphidophora*, remarking that "the uniform spongy equiaxial cells throughout the testa in the species are not fully in accord with the structure of *Epipremnum* as shown by Kirchheimer (1957, *pl. 12, fig. 54a*) and it seems probable that these seeds should be referred to the related genus *Rhaphidophora* (Dorofeev ex lit. 9.5.59)." Though the anatomy of these fossils may be at variance with that of modern *E. pinnatum*, their external morphology definitely excludes them from the genus

Rhaphidophora. This anatomical difference may arise from ecotypic variation or evolutionary modification, or it may represent a species-level distinction. With the exception of that reported by Kolesnikova (1960), the floras associated with this species are of a subtropical to warm-temperate East Asian affinity. While these floras do not entirely support the identification of the species, they do not disqualify it either.

Epipremnum uralense P. I. Dorofeev, Dokl. Akad. Nauk SSSR. 168: 685. *pl. 1, figs. 1–3*. 1966. [Oligocene]; Paleontol. Zhur. 2: 248. *pl. 17, figs. 9, 10*. 1968. [Oligocene]; Tretichnye flory Urala. [The Tertiary floras of the Ural.] Akad. Nauk SSSR., Bot. Inst. V. L. Komarova. 34. *pl. 5, figs. 4–6*. 1970. [Oligocene].

Anatropous seed, 2 × 2 mm., reniform, reflexed 140°–180°; nucellar end tapered and truncate, the chalazal end broadly rounded, and in lateral view the nucellar end longer than the chalazal end; surface smooth or pitted.

The morphology of this seed is close to that of *Scindapsus*, particularly *S. rupestris* (FIGURE 32). No further data are available to support this similarity, and the fossil might easily represent a separate or extinct species. The associated floras reflect a warm-temperate East Asian aspect, and (especially in Dorofeev, 1970) they may represent a mountainous flora within a generally warmer climate not unlike that of the present lower slopes of the Himalayas. The Mid to Late Oligocene has been interpreted as a period of expansion of the paleotropical elements of the European Tertiary, and it is not inappropriate to find members of the Monstereae in this type of flora.

Epipremnum species C. & E. M. Reid, Pliocene floras of the Dutch-Prussian border. 72. *pl. 4, figs. 13, 14*. 1915. [Pleistocene].

Anatropous seed, 1.3 mm. long, 2.2 mm. wide, reniform, reflexed 140°–180°; chalazal and nucellar ends of equal length, rounded; smooth surface faintly pitted, indicating raphide sacs.

With the exception of its smaller size, this fossil is an exact replica of the seed of *Epipremnum pinnatum* of the modern flora, but its presence in an interglacial deposit (Van der Hammen, 1951) makes it highly suspect. We retain it in this section of the discussion solely on the basis of the striking morphological similarity, but we suggest that it represents an unrecognized form masquerading as a monsteroid seed.

SPECIES ASSIGNABLE TO THE POTHOIDEAE

Araceites hungaricus K. Rásky, Ann. Hist.-Nat. Mus. Hungar. 56: 70. *pl. 9, fig. 5*. 1964. [Oligocene].

This well-preserved impression is a 2.5 cm. long and 1.2 cm. wide frag-

ment of a spadix possessing perfect flowers with a large central stigmatic region enclosed by a fused and reduced perianth. These characters suggest the Asian genus *Anadendrum*, to which fossil remains should perhaps be referred. *Anadendrum* is intermediate between the subfamilies Monsteroideae and Pothoideae, and, although Hutchinson (1959) referred it to the Monstereae, we follow Engler and Krause (1908) in referring it to the Pothoideae. The associated flora is subtropical and supports the generic assignment.

Species Assignable to the Lasioideae

Epipremnum cristatum P. A. Nikitin, Akvitanskaya flora Lagernogo Sada 7: 11–14. 1944. [not seen; cited by Dorofeev, 1952]: Akvitanskaya Semennaya flora Lagernogo Sada (Tomsk). Izdat. Tomskogo Universiteta. 64. *pl. 7, figs. 10–14.* 1965. [Tertiary].

Epipremnum cristatum Nikitin.

Bůžek, Č., & R. Holý, Sborn. Geol. Paleontol. **4:** 126. *pl. 6, figs. 10–13.* 1964. [Miocene].

Dorofeev, P. I., Bot. Zhur. **37:** 854. *pl. 2, figs. 13, 14.* 1952. [Pliocene]; Dokl. Akad. Nauk SSSR. **123:** 173. *pl. 1, fig. 8.* 1958. [Oligocene]; *Ibid.* **127:** 1104. 1959. [Oligocene]; *Ibid.* **144:** 650. 1962. [Miocene]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Siberia.] Izdat. Akad. Nauk SSSR. 132. *pl. 16, figs. 9–12.* 1963. [Tertiary]; Bot. Zhur. **51:** 1481. *pl. 1, fig. 43.* 1966. [Miocene].

Kolesnikova, T. D., Bot. Zhur. **45:** 119. *pl. 1, fig. 3.* 1960. [Miocene]; *Ibid.* **46:** 126. *pl. 1, fig. 3.* 1961. [Tertiary].

Palamarev, E., Bulgar. Akad. Wiss. Mitt. Bot. Inst. **20:** 61. *pl. 6, fig. 15*; *pl. 7, fig. 1.* 1970. [Miocene-Pliocene].

Szafer, W., Instyt. Geol. Prace. **33:** 93. *pl. 25, figs. 3–5.* 1961. [Miocene].

Carpolithus cristatus (Nikitin) D. H. Mai, Paläontol. Abhandl. B. **2:** 53. *text fig. 10*; *pl. 4, figs. 24, 25*; *pl. 6, fig. 12.* 1964. [Miocene].

Anatropous seed, 2.5–3.5 mm. long, 1.5–2.5 mm. wide, reniform, reflexed 90°–140°; chalazal end lower than the nucellar end in lateral view, the nucellar end flattened, the chalazal end tapered, both ends often bearing spines; dorsal and lateral faces bearing parallel ridges capped with strongly protuberant spines.

These distinctively spinose seeds are widely reported from the Tertiary of Europe and western Asia. With the exception of those illustrated by Palamarev, all of the figured forms definitely belong to the same specific entity. The seeds of *Epipremnum cristatum* do not resemble those of any extant species in the genus *Epipremnum* or those of any other monsteroid form seen by us. The prominent parallel rows of dorsal tubercles and the wide, flattened nucellar end are shared with a number of genera in the subfamily Lasioideae of the Araceae, including *Dracontioides*, *Dracontium*, and *Cyrtosperma*. Dorofeev (1963) has noted that *E. cristatum*

is only nominally assigned to *Epipremnum* and probably conforms more closely to *Cyrtosperma*. The exact disposition of *E. cristatum*, as with the following two species, must await an investigation of the seeds of the Lasioideae. The seed illustrated by Mai (1964) conforms to the morphology of *Epipremnum cristatum*, although he has labeled what is probably the chalazal end as the hilum.

The associated floras exhibit subtropical to warm-temperate affinities, with the exception of the flora described by Dorofeev (1952), which is cool-temperate. Although the Lasioideae are primarily tropical, some genera (e.g., *Amorphophallus*) extend as far north as Japan. The possible derivation of the forms of the European Tertiary from these northern species should not be overlooked.

Epipremnum rugosum P. I. Dorofeev, Dokl. Akad. Nauk SSSR. 137: 924. *pl. 1, fig. 18.* 1961. [Oligocene]; Tretichnye flory Zapadnoi Sibiri. [Tertiary floras of Western Siberia.] Izdat. Akad. Nauk SSSR. 132. *pl. 16, figs. 1–8.* 1963. [Tertiary].

Anatropous seed, approximately 3.8 × 3.5 mm., irregularly reniform; nucellar end flattened, the chalazal end tapered, and the two ends of approximately the same length in lateral view; dorsal surface showing numerous low, irregularly distributed small to large diameter tubercles.

The parallel rows of dorsal rugosities and the flattened nucellar end place the fossil in the subfamily Lasioideae, and Dorofeev (1963, p. 132) has noted that "this species is close to *Epipremnum cristatum* Nikitin, but it is undoubtedly independent. Perhaps it is another genus, for example, *Cyrtosperma*." This determination is only weakly supported by the warm-temperate, partly East Asian affinities of the associated floras.

Epipremnum visimense P. I. Dorofeev, Tretichnye flory Urala. [The Tertiary floras of the Ural.] Akad. Nauk SSSR., Bot. Inst. V. L. Komarova. 35. *text fig. 2; pl. 5, figs. 1–3.* 1970. [Oligocene].

Anatropous seed, about 2 × 2 mm., irregularly reniform, reflexed about 90°; nucellar end longer than the chalazal end in lateral view, the nucellar end flat, the chalazal end broadly rounded; two(?) low dorsal and two low dorsolateral mildly serrate ridges appearing as the only gross sculpture.

The affinities of this species lie with the subfamily Lasioideae, as indicated by the parallel dorsal and dorsolateral ridges and the broadly flattened nucellar end. Dorofeev (1970, p. 36) notes that the seed is only provisionally attributed to *Epipremnum* and is probably closer to *Cyrtosperma*. *Epipremnum visimense* is distinguished from *E. rugosum* and *E. cristatum* by its neatly parallel rows of low dorsal protuberances, in contrast to the unevenly distributed dorsal protuberances and larger size of

E. rugosum and the parallel but longer dorsal spines of *E. cristatum*. The presumed affinities of this seed with the Lasioideae are compatible with the warm-temperate to subtropical East Asian nature of the fossil floras with which it is associated.

SPECIES OF UNCERTAIN AFFINITY

Araceaeites parisiensis P. H. Fritel, Mém. Soc. Géol. France Paléontol. 40: 28. *text. fig. 15; pl. 3, fig. 1.* 1910. [Eocene].

Araceaeites fritelii E. W. Berry, U. S. Geol. Surv. Prof. Paper 91: 175. *pl. 114, figs. 3, 4.* 1916. [Eocene].

The genus *Araceaeites* was proposed for fossil spadices of Araceae and includes material of diverse affinities. We have already noted the similarity of *A. hungaricus* to the extant genus *Anadendrum*. The small (46 × 6 mm.) spadix of *A. parisiensis* figured by Fritel is compared by him to that of the modern genus *Spathiphyllum*. Though he mentions and figures what is probably the stigma of each flower, no mention is made of a possible perianth. The small size suggests *Spathiphyllum* or *Rhaphidophora* or even *Monstera*. Though apparently in the Araceae, the exact affinities of this specimen remain obscure. *Araceaeites parisiensis* is from the Lower Eocene of the Paris Basin and is associated with a strongly subtropical to tropical flora with East Asian affinities.

Araceaeites fritelii of the Eocene of the southeastern United States is so poorly preserved that it defies identification on the basis of published illustrations at ranks below the family level. The climate of the Eocene of the southeastern United States is characterized by Dilcher (1971, p. 18) as a "seasonally dry to slightly moist moisture regime and an equable warm temperate to cool subtropical temperature regime."

Acoropsis minor H. Conwentz, Die Flora des Bernsteins, II. Die Angiospermen des Bernsteins. 12. *pl. 1, figs. 14–17.* 1886. [Eocene].

Carex eximia Goeppert & Menge, Monatsber. Königl. Akad. der Wissenschaften Berlin. 459. 1853. [Eocene].

This fructification has been variously referred to *Carex* (Goeppert & Menge, 1853), *Acorus* (Araceae, Pothoideae; Conwentz, 1886), and the Monstereae (Bogner, pers. comm.). Kirchheimer (1957) felt that it lacked sufficiently distinctive characteristics to warrant identification, but examination of the illustrated material does suggest affinity with the Monstereae. The reader is referred to Bogner's forthcoming paper (in manuscript).

Cyrtospermites hordwellensis (Chandler) Bogner, Taxon 22: 321. 1973.

Campylospermum hordwellensis M. E. J. Chandler, The Upper Eocene flora of Hordle, Hants, I & II. Palaeontographical Soc. London. 16. *text. fig. 4*; *pl. 1, fig. 6a–c.* 1925 & 1926. [Eocene].

A seven(?)-seeded, thin-walled berry, with parietal placentation according to Chandler, 4 × 3.5–5 mm., the seeds 4 × 2 mm., reflexed approximately 180°; nucellar end longer than the chalazal end in lateral view, both rounded; surface of the seed obscured by the berry, but the raphal path on the arcuate ventral face clear.

This several-seeded berry was initially described as the fossil genus *Campylospermum*, which is a later homonym of a genus in the Ochnaceae. The required new name was supplied by Bogner in 1973. The form of the seed suggests that the species belongs to the Monsteroideae or Lasioideae, but the available characteristics do not allow any further distinctions. The affinity implied by the name *Cyrtospermites* is unfortunate, since the seeds possess no characteristic that definitely links them to the modern genus *Cyrtosperma*. The associated flora is tropical to subtropical, with strong East Asian affinities.

Epipremnum reniculum (Ludwig) F. Kirchheimer, Bot. Jahrb. **67**: 79. *pl. 11, fig. 33a–i.* 1935. [Oligocene].

Epipremnum reniculum (Ludwig) F. Kirchheimer.

Dorofeev, P. I., Bot. Zhur. **45**: 1419. *pl. 3, figs. 5, 6.* 1960. [Oligocene]; Nizhniĭ Pleĭstotsen Lednikovykh Raĭonov Russkoĭ Ravniny. Akad. Nauk SSSR. Kom. po Izuch. Chetvertichnogo Perioda. *pl. 2, figs. 13, 14.* 1967. [Pleistocene].

Cytisus reniculus Ludwig, Palaeontographica B. **5**: 101. *pl. 20, fig. 21.* 1857. [Pliocene].

Carpolithus reniculus (Ludwig) P. Menzel, Jahrb. Preussisch. Geol. Landesanstalt **34**: 19. *pl. 1, fig. 37.* 1913. [Oligocene].

Kirchheimer, F., Das Hauptbraunkohlenlager der Wetterau. 36. *pl. 9, figs. 7–10.* 1934. [Pliocene]; Die Laubgewächse der Braunkohlenzeit. 113, 348. *pl. 12, figs. 53, 54.* 1957. [Oligocene].

Mai, D. H., Paläontol. Abhandl. B. 2: 53. *pl. 4, figs. 26, 27.* 1964. [Miocene].

Carpolithus reniformis V. Fritsch, Jahrb. Preussisch. Geol. Landesanstalt **5**: 437. *pl. 26, fig. 26.* 1884. [Pliocene].

Anatropous seed, 2.5 mm. long, 1.5–2 mm. wide, reniform to cordate, reflexed 120°–160°, the ventral hollow small or lacking, giving the seed a rounded appearance, the round to slightly flattened nucellar end as long as the round to tapered chalazal end in lateral view; surface smooth.

The systematic placement of this species is uncertain. Although Dorofeev (1960) accepted it as *Epipremnum*, Kirchheimer (1957) referred it to the form genus *Carpolithus*, noting its strong resemblance to the seeds of *Kitaibelia vitifolia* (Malvaceae) and *Cytisus* (Leguminosae). Simul-

taneously he enlarged the species concept to include the fossils described as *E. crassum* Reid & Reid.

The size, general outline, prominent micropyle, and external pitting of many of these fossils does suggest *Epipremnum*, but the fossils do not closely match the seeds of any extant species. Those illustrated by Mai (1964) are interpreted by him as possessing a micropyle and hilum on opposite ends of the seed; if this is correct, the fossil is definitely excluded from the Monstereae. Kirchheimer's (1957) sections of modern *Epipremnum pinnatum* reveal a thin-walled testa composed of elongate sclereids, whereas the fossil possesses a thick testa of isodiametric ones.

The floras accompanying these fossils range from subtropical to interglacial. The anatomical distinctions and the varied climatic relations of this species suggest that few, if any, of its assigned members belong to the Araceae.

Epipremnum sp. 3? P. A. Nikitin, Akvitanskaya Semennaya flora Lagernogo Sada (Tomsk). Izdat. Tomskogo Universiteta. 65. *pl. 7, fig. 15.* 1965. [Tertiary].

This small (1.62 × 1.04 mm.) seed is the wrong shape to be that of a modern *Epipremnum*, and it possesses a medial perforation not seen in the seeds of any of the modern species. It may be excluded from the genus and perhaps from the family.

Aracispermum Nikitin.

A genus comprising at least six species, with ovoid to elongate-ovoid orthotropous seeds ranging from 1 to 4 mm. in length and 1 to 2 mm. in diameter; seeds externally smooth or longitudinally furrowed, the base rounded to pointed and the apex with a conical depression leading to an internal cavity.

Mai (1964) observed that the characters of these seeds, particularly of the central cavity and the apical "micropylar canal," suggest the families Araceae or Zingiberaceae. However, both he and Lańcucka-Środoniowa (1966) note that no comparable modern genus is known. We cannot offer suggestions as to the identity of these seeds, but they can definitely be excluded from the Monstereae.

DISCUSSION

In the Monstereae there is a correlation of seed size, seed curvature, and relative abundance of endosperm, ranging from small uncurved seeds with abundant endosperm to large, highly curved seeds lacking endosperm. These seem to represent a simple allometric series, although the seeds of *Rhodospatha* are somewhat smaller than would be expected for their degree of curvature in the context of the tribe as a whole, and those

of *Amydrium* are somewhat larger. The extant genera occupy discrete intervals in this series, and seed morphology is a useful generic character, particularly in separating *Rhaphidophora*, *Epipremnum*, and *Monstera*, many species of which are very similar in other respects.

The curvature of the seeds appears to be a consequence of the slower growth of the funiculus and raphe in relation to the elongation of the rest of the seed. Large *Monstera* seeds require a year to develop; it is not surprising that the heavily vascularized raphe cannot continually elongate during that time. The static length of the raphe coupled with the continuing growth of the rest of the seed in the confines of a narrow ovary necessarily results in curvature of the seed about the raphe.

The presence or absence of endosperm in the mature seed seems to depend on the relative growth rates of the embryo and endosperm. In large seeds the relatively faster growing embryo consumes the endosperm by maturity, whereas in smaller seeds the embryo growth rate is slower and maturity is achieved prior to the consumption of the endosperm. In the developing *Monstera* seed the endosperm is initially dominant, but the developing embryo soon consumes the endosperm at a more rapid rate than it is produced. By the time the seed has become curved, but prior to the initiation of dorsal elongation, the endosperm constitutes about one fifth of the volume of the seed. This remaining endosperm is consumed during the final dorsal elongation. The possibility of a neotonic derivation of *Epipremnum*-like forms from *Monstera* must be discounted. In *Epipremnum* the embryo is axile and surrounded by a sheath of endosperm, whereas in *Monstera* all of the endosperm at the nucellar end is consumed during the early stages of growth and the embryo then contacts the endosperm on only one face as the seed curves and enlarges.

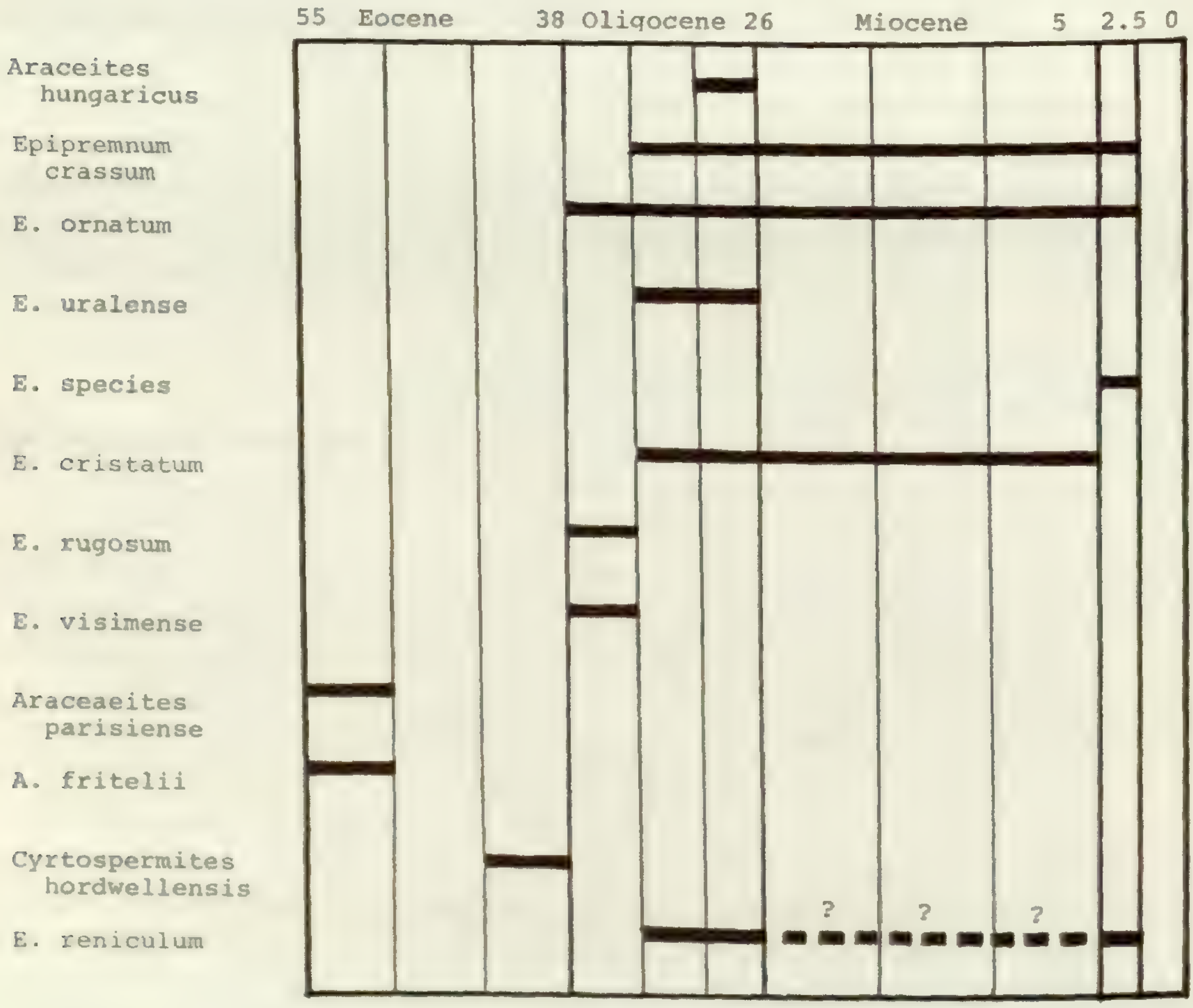
The fossil seeds which we accept as *Epipremnum* readily fit into the morphological sequence evident in the extant species of Monstereae. In addition, they resemble modern species of *Epipremnum* in the pitting of the surface. However, the associated vegetative or fruiting remains necessary for an unequivocal generic identification of these fossils are lacking, and the possibility exists that some modern group unrelated to the Araceae may be found to have a similar seed morphology.

The considerable geographic and stratigraphic range of these fossils is worthy of note. The low number of described Eocene Araceae is surprising in view of the known Eocene maximum of paleotropical elements in the European flora (Mai, 1965; Reid & Chandler, 1933). The greatest number of coexisting species of fossil Araceae (seven) occur in the Oligocene, concomitant with the last major advance of the paleotropical flora into Europe (Mai, 1965). This number drops to three species at the Oligocene-Miocene border with the commencement of the retreat of the thermophilic floras. The "warm temperate, subtropical and rather humid" climate suggested by Schwarzbach (1966) for the European Late Oligocene to Mid Miocene gave way to increasing cooling and aridity in the Late Miocene and Pliocene, presumably causing the retreat or extinction of tropical Araceae from Europe.

The present-day distribution of the Monstereae is primarily neotropical and Indomalesian, with two species in West Africa, and it ranges from 27° south latitude to 28° north latitude. The most nearly extratropical members of the tribe are *Rhaphidophora* and *Scindapsus*, which ascend to 2000 m. in the Himalayas, and *Monstera*, which in northern Central America occurs in cool forests at 2500 m. *Monstera deliciosa* persists in subtropical Florida, although it is not native there. The floras associated with the fossil Monstereae range from tropical and subtropical to warm-temperate. While these floras are not altogether incompatible with the ecological tolerances of modern Monstereae, they suggest that some of the fossilized forms may represent individuals at the edge of their range. It is also conceivable that extinct Monstereae had a wider ecological amplitude than modern species.

Engler and Krause (1908) proposed that the neotropical Monstereae were derived from the paleotropical forms. The existence of seeds of this tribe in European and Siberian Tertiary deposits as far as 50° to 55° north latitude suggests that the group once had a more cosmopolitan distribution than at present. The paucity of reported New World fossil material may reflect less intensive sampling or the absence of the family in the Paleogene of the New World. If future work reveals North American fossil material,

TABLE 1. **Distribution of the fruiting remains of the Araceae (excluding Aracispermum Nikitin) in the fossil record. Time in millions of years.**



then the similarities of the African and South American forms could be ascribed to a common derivation from a Paleogene Boreotropical flora, in keeping with Wolfe's (1975) hypothesis. If, however, the tribe is absent from the New World Paleogene, the present day paleotropical forms might have been derived from a common European-Asian Paleogene Boreotropical flora, and the South American forms might subsequently have been derived from the African ones.

ACKNOWLEDGMENTS

The authors wish to express their gratitude to Ms. Kate Roby for the translation of passages from the Russian literature. Thanks are also due to Dr. Elisabeth Wheeler of Harvard University, Drs. Richard Eyde and Dan Nicolson of the Smithsonian Institution, and Dr. Josef Bogner of the Munich Botanical Garden for their valuable comments and suggestions.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1–6. Representative seeds of six extant genera of the tribe Monstereae; lateral and ventral views: 1, *Stenospermation* sp., Ecuador, *Madison 908* (GH), × 10; 2, *Rhaphidophora monticola*, Philippines, *Wenzel 1160* (GH), × 9; 3, *Epipremnum pinnatum*, Hainan, *Ko 52235* (GH), × 4.5; 4, *Rhodospatha* sp., Colombia, *Schultes & Cabrera 18958* (GH), × 13; 5, *Scindapsus officinalis*, Thailand, *Nicolson 1683* (A), × 3; 6, *Monstera dubia*, Colombia, *Madison 826* (GH), × 2. (c = chalaza; h = hilum; m = micropyle; r = raphe.)

FIGURE 7. Developmental stages in the growth of the seed of *Monstera dubia*, Colombia, *Madison 826* (GH), × 2; lateral view.

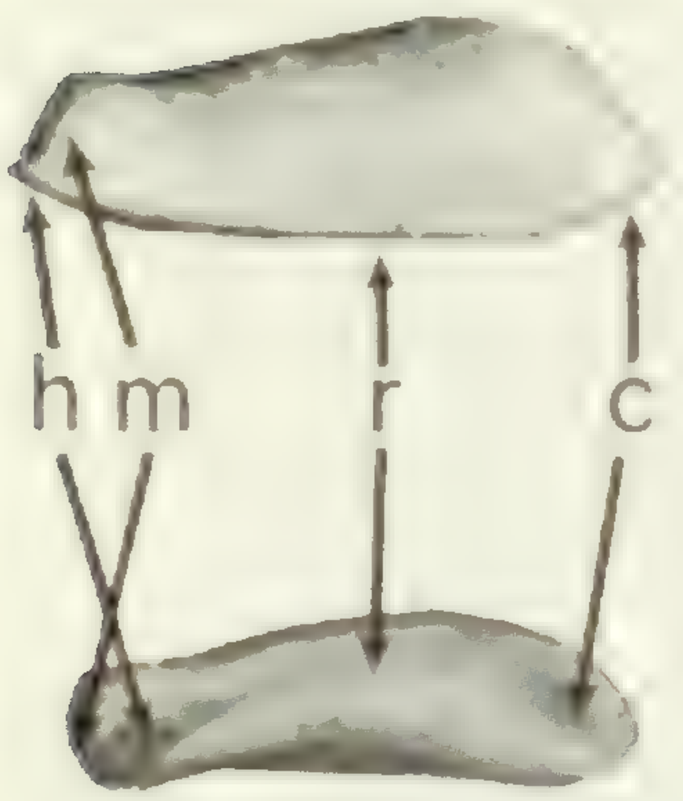
PLATE II

FIGURES 8–34. Seeds of *Stenospermation*, *Rhaphidophora*, *Epipremnum*, *Rhodospatha*, and *Scindapsus*: 8, *Stenospermation* sp. Ecuador, *Madison 908* (GH), × 7.5; 9, *S. sessile*, Panama, *Duke & Dwyer 13969* (GH), × 7.5; 10, *Rhaphidophora affinis*, Burma, *Dickason 5017* (GH), × 7.5; 11, *R. bulusanensi*, Philippines, *Elmer 16790* (GH), × 7.5; 12, *R. decursiva*, Laos, *Poilane 20636* (A), × 7.5; 13, *R. grandis*, China, *Wang 74405* (A), × 7.5; 14, *R. grandis*, New Hebrides, *Kajewski 830* (A), × 7.5; 15, *R. monticola*, Philippines, *Wenzel 1160* (GH), × 7.5; 16, *R. reineckei*, Samoa, *Bryan 115* (GH), × 7.5; 17, *R. trinerva*, Philippines, *Elmer 18057* (GH), × 7.5; 18, *R. yunnanensis*, China, *Wang 74120* (A), × 7.5; 19, *Rhaphidophora* sp., Thailand, *Nicolson 1655* (A), × 7.5; 20, *Rhaphidophora* sp., Burma, *Dickason 7823* (A), × 7.5; 21, *Epipremnum amplissimum*, W. New Guinea, *Van Royen 3123* (A), × 3; 22, *E. elegans*, Solomon Islands, *RSS 2330* (A), × 3; 23, *E. pinnatum*, Hainan, *Ko 52235* (GH), × 3; 24, *E. pinnatum*, Solomon Islands, *Brass 2755* (A), × 3; 25, *Epipremnum* sp., New Guinea, *Hartley 10259* (A), × 3; 26, *Rhodospatha* sp., Colombia, *Schultes & Cabrera 18958* (GH), × 7.5; 27, *R. latifolia*, Ecuador, *Madison 921* (GH), × 7.5; 28, *Scindapsus altissimus*, Papua, *Brass 8185* (A), × 3; 29, *S. hederaceus*, Sumatra, *Bangham 1271* (GH), × 3; 30, *S. maclurei*, Thailand, *Nicolson 1642* (A), × 3; 31, *S. officinalis*, Burma, *Dickason 5510* (GH), × 3; 32, *S. rupestris*, Borneo, *Clemens 31094* (A), × 3; 33, *S. subcordatus*, Papua, *Brass 7269* (A), × 3; 34, *Scindapsus* sp., Papua, *Brass 13031* (A), × 3.

PLATE III

FIGURES 35–47. Seeds of *Monstera*, *Amydrium*, and *Anadendrum*: 35, *Monstera acuminata*, Mexico, *Madison 1782* (GH), × 2; 36, *M. adansonii* var. *laniata*, Colombia, *Madison 819* (GH), × 2; 37, *M. deliciosa*, Guatemala, *Madison 657* (GH), × 2; 38, *M. dilacerata*, Colombia, *Madison 1213* (GH), × 2; 39, *M. dubia*, Ecuador, *Madison 905* (GH), × 2; 40, *M. lechlerana*, Colombia, *Madison 871* (GH), × 2; 41, *M. membranacea*, Costa Rica, *Madison 738* (GH), × 2; 42, *M. punctulata*, Mexico, *Madison 633* (GH), × 2; 43, *M. siltepecana*, Guatemala, *Madison 661* (GH), × 2; 44, *M. tuberculata*, Costa Rica, *Madison 752* (GH), × 2; 45, *Amydrium magnificum*, Papua, *Brass 25015* (A), × 2.5; 46, *Anadendrum microstachyum*, Java, *Van Steenis 12642* (A), × 2.5; 47, *A. latifolium*, Viet Nam, *Poilane 6384* (A), × 2.5.

FIGURES 48–51. Araceous fossil seeds from Russian Tertiary deposits: 48, *Epipremnum ornatum* Reid & Chandler. *In*: A. L. Takhtajan, ed., Osnovy paleontologii. [Fundamentals of paleontology.] Vol. 15. Acad. Sci. SSSR. Moscow. 632. *fig. 398d*. 1963. [Tertiary], × 4.2; 49, *Epipremnum cristatum* Nikitin. *In*: *Ibid. fig. 398b*. 1963. [Tertiary], × 4.2; 50, *Epipremnum visimense* P. I. Dorofeev, Tretichnye flory Urala. [Tertiary floras of the Ural.] Botanical Institute V. L. Komarova. 35. *fig. 2*. 1970. [Oligocene], × 7.3; 51, *Epipremnum crassum* C. & E. M. Reid. *In*: P. I. Dorofeev, O Pliotsenovoi flory Bashkirskogo Predvral'ya. [The Pliocene floras of the Bashkirian foothills of the Urals.] Bask. Fil. Akad. Nauk SSSR. 18. *pl. 3, fig. 3*. 1960. [Pliocene], × 7.5.



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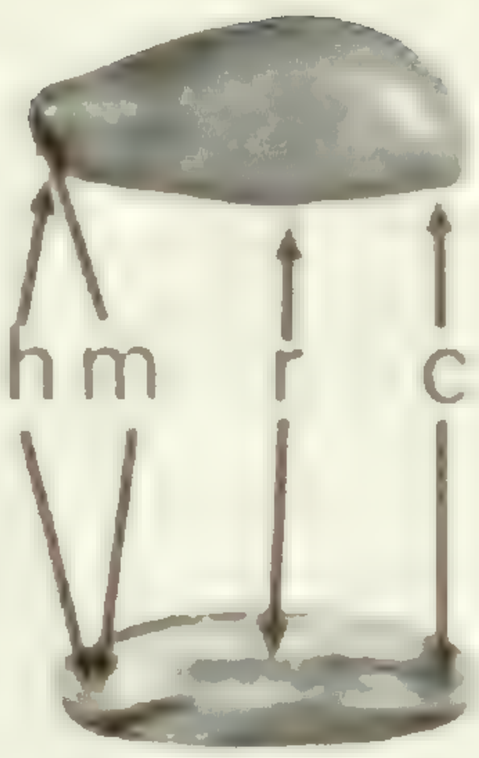

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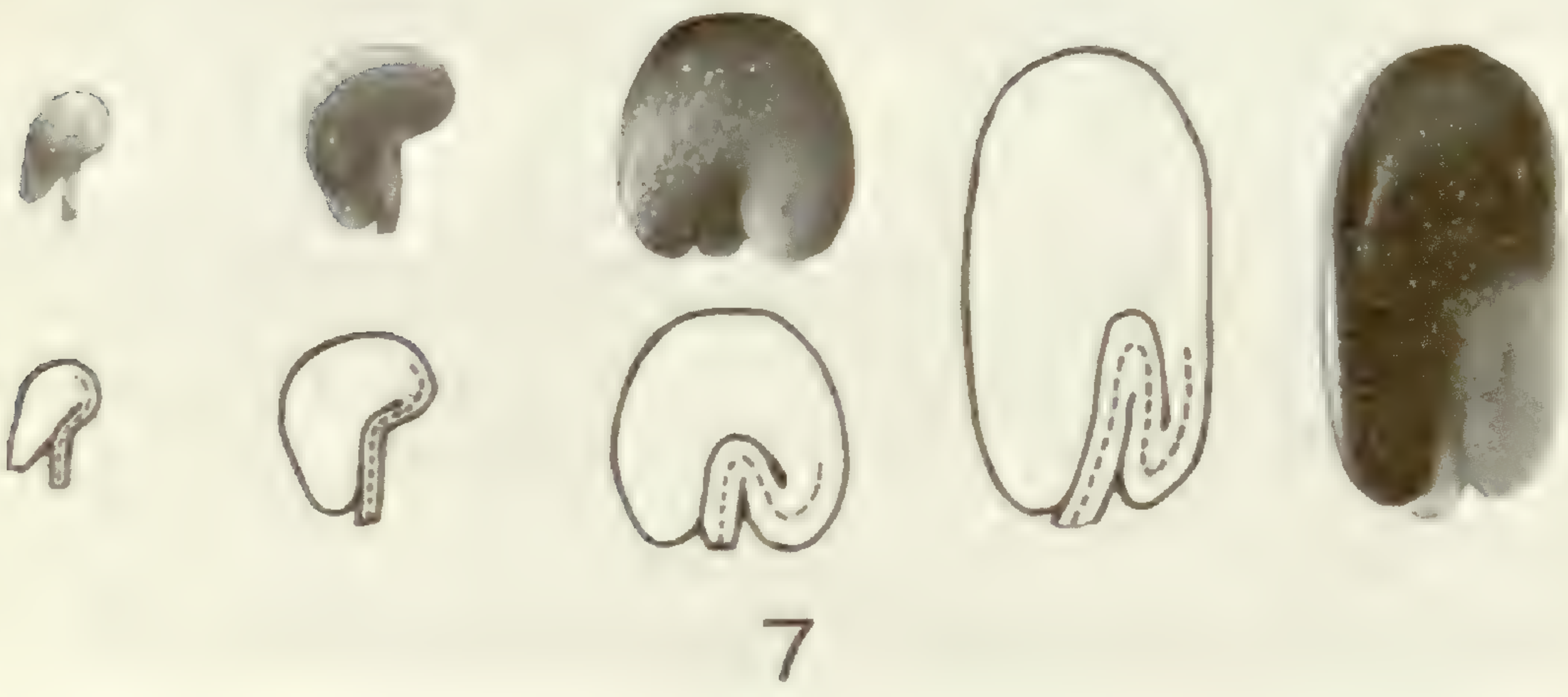

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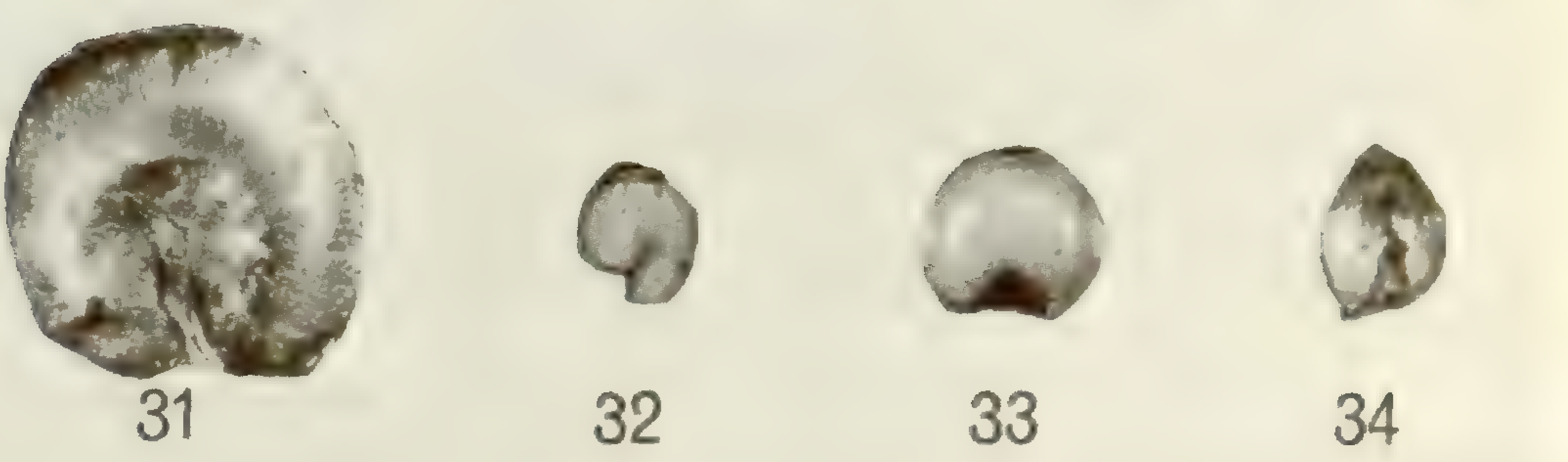

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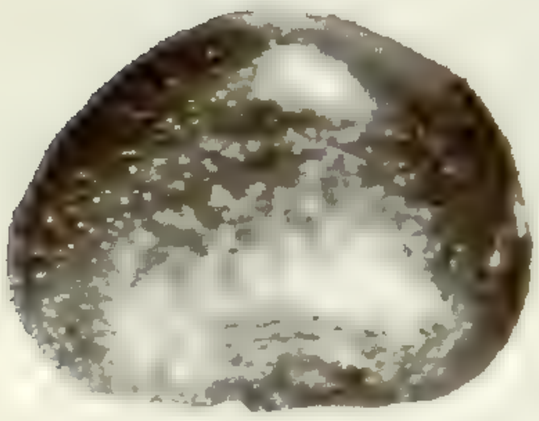

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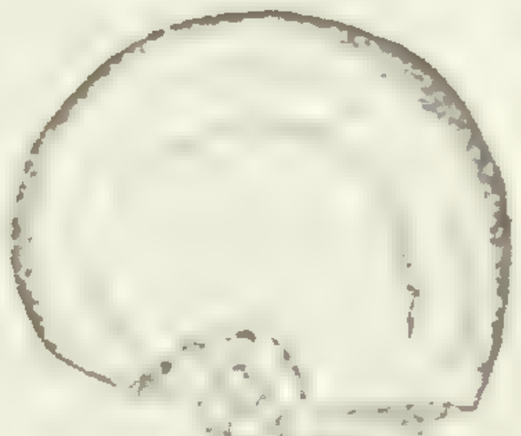

51

THE GENERA OF HAEMODORACEAE IN THE SOUTHEASTERN UNITED STATES [1]

KENNETH R. ROBERTSON

HAEMODORACEAE R. Brown, Prodr. Fl. Nov. Holland 1: 299. 1810, nom. cons.

(BLOODWORT FAMILY)

Perennial [or rarely annual], rhizomatous and often stoloniferous herbs; above-ground stem simple, terminating in an inflorescence; roots fibrous; sap often red or orange. Stems, inflorescence branches, and floral tubes often covered with simple [branched or glandular] trichomes. Leaves alternate, mostly basal, *Iris*-like, linear [or narrowly elliptical], flattened [or subcylindrical], 2-ranked, sheathing below, folded lengthwise above, with the folded portions becoming fused together (see FIGURE 2, b–e). Inflorescences much-branched, many-flowered, loose or condensed cymes or corymbs [panicles or racemes, rarely solitary flowers] terminating the aerial stem and exceeding the leaves; bracts present, often conspicuous and persistent. Flowers regularly [or irregularly] symmetrical, 3-merous, the insertion of the perianth and androecium epigynous, perigynous [or hypogynous]. Tepals 6 in 2 whorls [or 1 whorl], ± equal to unequal, free to level of insertion on the ovary [or united into a tube that may be split along one side], valvate in aestivation, persistent in fruit. Androecium of 6 or 3 stamens [or some reduced to staminodes]; filaments elongate [or very short], free to level of insertion on ovary [or adnate to perianth tube]; anthers 2-loculate, basifixed, dehiscing introrsely by longitudinal slits, often basally sagittate [sometimes also apiculate]; tapetum amoeboid; pollen grains produced successively. Gynoecium of 3 united carpels; ovary inferior or half-inferior [or superior], 3-locular with

[1] Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation, currently under Grant BMS74–21469 (Carroll E. Wood, Jr., principal investigator). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958). The area covered includes North Carolina, South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References that I have not seen are marked by an asterisk.

The illustration of *Lachnanthes* was drawn by Virginia Savage under the supervision of C. E. Wood, Jr., who also collected the material on which it is based. Karen S. Velmure drew the plate of *Lophiola* under my direction from material collected by R. E. Umber and me.

I want to thank Professor Wood for his continuing advice and suggestions and for information about the correct name of *Lachnanthes caroliana*. The manuscript was typed by Beverly Vincent.

axile placentae or 1-locular with parietal placentae above and 3-locular with axile placentae below; style 1, undivided [or 3-parted above], elongate [to short]; stigmatic area terminal, very small; ovules orthotropous or anatropous, crassinucellar, few [or 1] or numerous in each locule, arranged in vertical rows or around the margin of a peltate placenta [or covering it]. Fruit a loculicidal [or septicidal or septifragal] capsule [or rarely indehiscent]. Seeds discoid and peltate or elongate and variously curved [or ovoid or flattened]; endosperm present, helobial in development. Embryo sac development of the Polygonum type. TYPE GENUS: *Haemodorum* J. E. Smith.

The subfamilial classification and the number of genera included in the family vary considerably with different authors. In the recent worldwide review by Geerinck, two tribes, 13 genera, and about 76 species were recognized. Six genera are monotypic, and only three have more than ten species. Five genera are restricted to Oceania (particularly Australia), three to South Africa, two to eastern North America, and two to South America; one is widespread from Bolivia and Brazil to Cuba and Mexico. *Lachnanthes* and *Lophiola*, both probably monotypic, occur in the southeastern United States.

The nomenclatural history of the family is too involved to give in detail,[2] but the following account is relevant to the discussion of the genera in the southeastern United States. The family was established by Robert Brown, who divided it into three unnamed sections, with *Haemodorum* in the first, *Conostylis* R. Br. and *Anigozanthos* Labill. in the second, and *Phlebocarya* R. Br. in the third. Bentham, in Volume 6 of the *Flora Australiensis* (1873), placed the genera previously assigned to the Haemodoraceae in tribes Haemodoreae and Conostylideae ("Conostyleae") of the Amaryllidaceae. In the *Genera Plantarum*, however, Bentham & Hooker recognized the Haemodoraceae, considering the family to be composed of 26 genera in four tribes, Euhaemodoreae, Conostylideae, Ophiopogoneae, and Conanthereae. As delimited by Bentham & Hooker, the family was not a natural assemblage. Pax (and Pax & Hoffmann), in both editions of Engler & Prantl's *Pflanzenfamilien*, restricted the Haemodoraceae largely to the genera previously referred to tribe Haemodoreae, placing tribes Conostylideae and Conanthereae in the Amaryllidaceae and tribe Ophiopogoneae in the Liliaceae. Hutchinson (1973) disagreed with Pax, saying, "After a careful examination of all the genera of both families I cannot agree with this treatment, and I am firmly of the opinion that the two tribes [Haemodoreae and Conostylideae] should be again associated to form the Haemodoraceae. Thus constituted, but with the genus *Aletris* L. removed to the Liliaceae, the family is natural and homogeneous, not only in its facies but in its general distribution."

[2] See table in Geerinck (1969) for an extremely useful outline of the genera that have been included in the Haemodoraceae and Hypoxidaceae, with the taxonomic disposition of each genus by family, subfamily, and tribe from seventeen different works.

Conanthera and related genera were placed by Hutchinson in the segregate family Tecophilaeaceae (Liliales). Geerinck's concept of the family is essentially the same as Hutchinson's, except that Geerinck questionably excludes *Lanaria* Aiton from the Haemodoraceae and places *Lophiola* in tribe Haemodoreae instead of tribe Conostylideae. Melchior returns to the broad concept of the family and recognizes three tribes, Haemodoreae, Conostylideae, and Conanthereae.

Lachnanthes clearly belongs to tribe Haemodoreae and, on morphological grounds, seems to be most closely related to *Haemodorum* (20 species of Oceania) and *Dilatris* Berg. (five species of South Africa). The relationships of *Lophiola*, however, are not clear; it has often been included in tribe Conostylideae. The other members of this tribe are confined to southwestern Australia, and *Lophiola* really does not have much in common with them. Geerinck places *Lophiola* next to *Lachnanthes* in tribe Haemodoreae. While these two genera are superficially quite similar, the morphological differences between them are numerous, and it seems doubtful that they are closely related. De Vos (1963) has recently pointed out numerous similarities between *Lophiola* and *Lanaria*, a monotypic genus of South Africa that has been placed in the tribe Haemodoreae, the tribe Conanthereae, or the family Tecophilaeaceae. As far as is presently known, the two genera of Haemodoraceae in eastern North America do not seem to have any close relatives in the West Indies, Central America, or South America.

As mentioned above, *Aletris* (perhaps 25 species of eastern North America and eastern Asia) was included in the Haemodoraceae by Bentham & Hooker. It is commonly recognized today, however, that this genus is best included in the Liliaceae. *Sansevieria* Thunb. (about 60 species of the Old World), also included in the Haemodoraceae by Bentham & Hooker, is now usually placed in the Liliaceae or Agavaceae; *S. thyrsiflora* Thunb. is naturalized in southern Florida.

The Haemodoraceae, as delimited by Geerinck, contain two pollen types (see Erdtman). The pollen of tribe Haemodoreae is 1-sulcate, while that of tribe Conostylideae is 2–8-aperturate (often 3-aperturate). Erdtman comments that "the occurrence of 3-aperturate grains in Hypoxidoideae-Conostylideae [= Haemodoraceae tribe Conostylideae of this paper] excludes the possibility of assigning 3-aperturate pollen grains to Dicotyledoneae merely on the basis of aperture number." Other monocotyledonous families in which 3-aperturate pollen occurs are the Alismataceae, Araceae, and Bromeliaceae. Erdtman noted that *Lanaria* and *Lophiola* are palynologically more similar to tribe Conanthereae (perhaps best treated as the Tecophilaeaceae) than to the Haemodoraceae *sensu* Pax.

Little is known about breeding systems or pollination and dispersal mechanisms in the family. Some South African Haemodoraceae exhibit a type of enantiostyly, with morphologically different "left-" and "right-handed" flowers (see Barker, Ornduff, and Wilson). The flowers of *Anigozanthos* often have bright, contrasting colors, such as red, yellow, vivid green, blue, and black (an unusual color in flowers), and are

mostly pollinated by birds (honeyeaters, family Meliphagidae). The strange, discoid seeds of *Lachnanthes* and *Haemodorum* are probably dispersed by wind. In *Dilatris corymbosa* Berg. and *D. Pillansii* Barker, the persistent perianth atop the indehiscent fruit acts as a parachute (see Barker). Reported sporophytic chromosome numbers are: *Anigozanthos* (including *Macropidia* Harv.), 12 (6 species), and *Conostylis* R. Br. (including *Blancoa* Lindl.), 8, 10, 14, 16, and 28 (a total of 17 species examined). *Lachnanthes* and *Lophiola* are cytologically unknown.

Annotations of specimens in the combined herbaria of the Arnold Arboretum and the Gray Herbarium of Harvard University indicate that A. Stoel, of Utrecht, is preparing a revision of the New World Haemodoraceae.

Except for the occasional cultivation of some species (especially of *Anigozanthos*) as curiosities, the family is of little economic importance. A tincture of the roots of *Lachnanthes caroliana* was used by American Indians as an invigorating tonic and as an herb remedy.

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KEY TO THE GENERA OF HAEMODORACEAE IN THE SOUTHEASTERN UNITED STATES

A. Stamens 3, exserted; ovary inferior, insertion of tepals and stamens epigynous; tepals glabrous adaxially; seeds few in each locule, reddish brown, peltate, orbicular in outline, strongly flattened. ..... 1. *Lachnanthes*.
A. Stamens 6, about equalling tepals; ovary half-inferior, insertion of tepals and stamens perigynous; tepals with an adaxial crest of yellow, uniseriate multicellular trichomes; seeds numerous in each locule, whitish, tiny, elongate, variously curved, the hilum basal. ..... 2. *Lophiola*.

1. **Lachnanthes** S. Elliott, Sketch Bot. S. Carolina Georgia 1: 47. 1816. ('1821'), **nom. cons.**

Stout perennial herbs with reddish rhizomes and fibrous roots; sap red. Upper portions of stem, inflorescence branches, and outer parts of flowers whitish villous-tomentose when young, becoming tawny hoary. Leaves mostly basal, sword-shaped, the cauline ones few and reduced in size. Inflorescences terminal on stem, many-flowered, initially compact and rounded, becoming open and corymbose after anthesis, with each branch resembling a helicoid cyme; bracts conspicuous, subtending each flower. Flowers regularly symmetrical, the insertion of the tepals and stamens epigynous. Tepals 6 in 2 whorls of 3, free to level of insertion, pale yellow, erect-spreading at anthesis, inserted around the top of the ovary, densely pubescent abaxially, glabrous adaxially, valvate in aestivation, the outer 3 narrower and slightly shorter than the inner 3. Stamens 3, exserted, erect-spreading at anthesis; filaments inserted on the top of the ovary opposite the inner whorl of tepals, persistent in fruit and then enclosed by the inrolled margins of the inner tepals; anthers yellow, introrse, basifixed, very slightly sagittate below, curving outward after dehiscence. Ovary inferior, 3-locular; style slightly exceeding the anthers, persistent in fruit; stigmatic area faintly 3-lobed; ovules about 6 per locule, inserted around the margin of a peltate, stipitate, axile placenta. Capsule globose or oblate, capped by the persistent tepals, dehiscent by 3 loculicidal valves, the style not attached to the fruit valves but remaining on the columella or breaking off. Seeds discoid, peltate, reddish brown, few per locule, attached around the placenta; seed coat faintly wrinkled. (Including *Heritiera* J. F. Gmelin, 1791, neither Aiton, 1789, nor Retzius, 1791, nor *Heriteria* Schrank, 1789; *Gyrotheca* Salisb.; *Camderia* Dumortier.) TYPE SPECIES: *L. tinctoria* S. Elliott = *L. caroliana* (Lam.) Dandy. (Name from Greek *lachne*, wool, and *anthos*, flower, in reference to the pubescent flowers.) — REDROOT.

One species of scattered distribution in eastern North America, occurring in southern Nova Scotia; Rhode Island and southeastern Massachusetts; the pine barrens of New Jersey and Delaware; southeastern Virginia; Augusta County, Virginia; Coffee County, Tennessee; and on the Atlantic and Gulf coastal plains from North Carolina south to southern Florida, westward through the panhandle of Florida to Saint Tammany

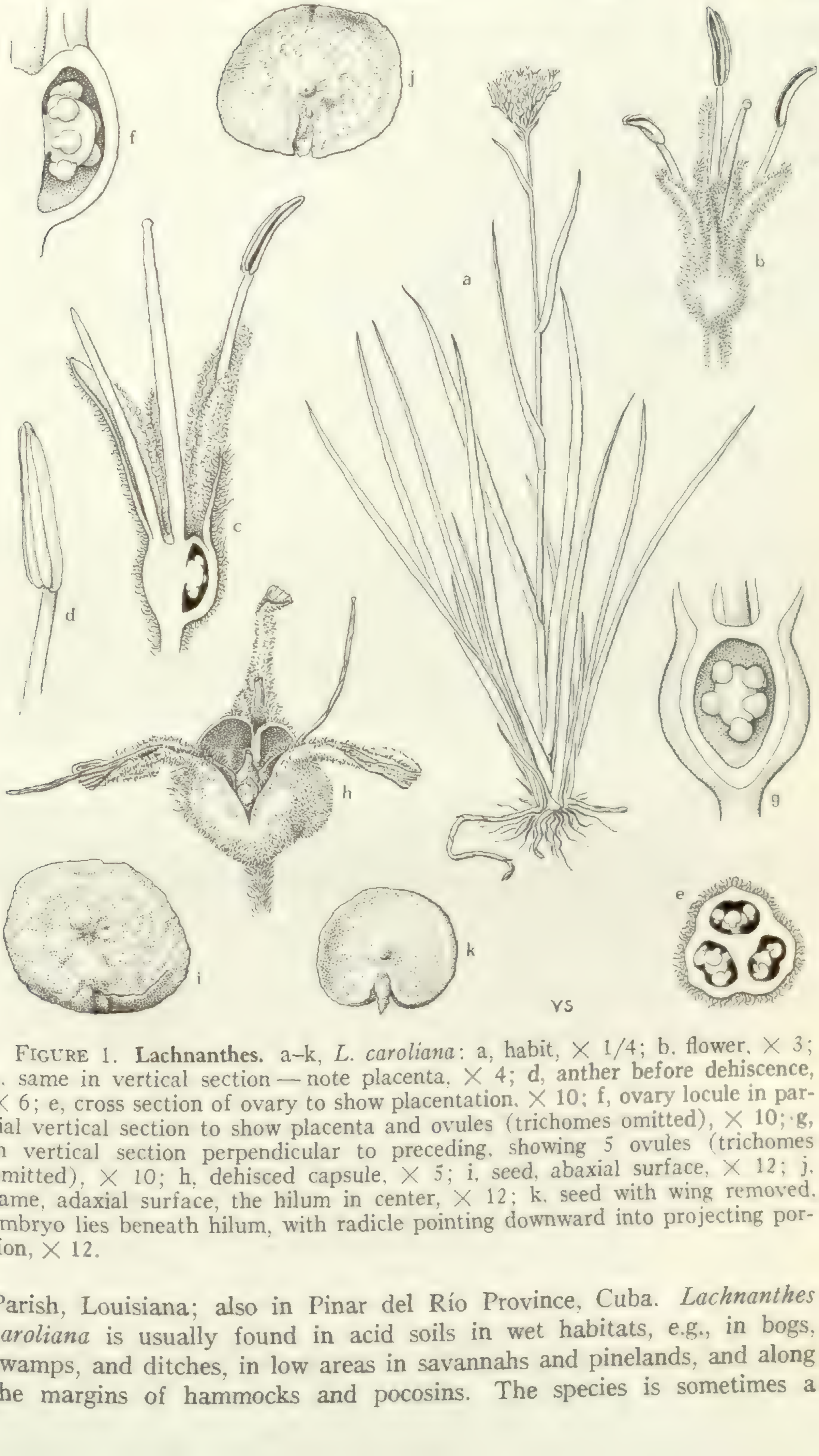

FIGURE 1. **Lachnanthes.** a–k, *L. caroliana*: a, habit, × 1/4; b, flower, × 3; c, same in vertical section — note placenta, × 4; d, anther before dehiscence, × 6; e, cross section of ovary to show placentation, × 10; f, ovary locule in partial vertical section to show placenta and ovules (trichomes omitted), × 10; g, in vertical section perpendicular to preceding, showing 5 ovules (trichomes omitted), × 10; h, dehisced capsule, × 5; i, seed, abaxial surface, × 12; j, same, adaxial surface, the hilum in center, × 12; k, seed with wing removed, embryo lies beneath hilum, with radicle pointing downward into projecting portion, × 12.

Parish, Louisiana; also in Pinar del Río Province, Cuba. *Lachnanthes caroliana* is usually found in acid soils in wet habitats, e.g., in bogs, swamps, and ditches, in low areas in savannahs and pinelands, and along the margins of hammocks and pocosins. The species is sometimes a

rather aggressive weed in commercial cranberry (*Vaccinium macrocarpon*) bogs.

A number of names have been applied to this plant, including (orthographic variants omitted) *Anonymos tinctori*[*a*] Walter, *Dilatris caroliana* Lam., *Heritiera tinctorum* J. F. Gmelin, *Heritiera Gmelini* Michx., *Dilatris Heritiera* Persoon, *D. tinctoria* Pursh, *Lachnanthes tinctoria* Elliott, *Gyrotheca tinctoria* Salisb., and *Gyrotheca capiata* Morong. The generic name *Lachnanthes* is now conserved, and the earliest specific name is *Dilatris caroliana* Lam., Tabl. Encycl. Méth. Bot. 1: 127. 1791 (March), which is earlier than the next available name, *Heritiera tinctorum* J. F. Gmelin, Linn. Syst. Nat. ed. 13. 2: 113. 1791 (Sept./Nov.). Thus the correct combination for this plant is *Lachnanthes caroliana* (Lam.) Dandy, Jour. Bot. 70: 329. 1932.

Although a photograph of the type specimen of *Dilatris caroliana* Lam. in the Herbier Lamarck, Muséum National d'Histoire Naturelle, Paris, shows the name as "*Dilatris caroliniana*" on the label, Lamarck published the name as *D. caroliana*. This has been considered by some to be an orthographic error. According to Wilbur, "the epithet originally appeared as '*caroliana*,' but Dr. Shinners has kindly pointed out that this was an obvious misprint and hence is to be corrected under the provisions of Art. 73" of the International Code of Botanical Nomenclature. It seems to the present author, however, that we are obliged to maintain the spelling of the original publication.

The occurrence of *Lachnanthes caroliana* inland on the western slope of the Blue Ridge in Augusta County, Virginia, and in the "oak-barren" country of central Tennessee (Coffee County) is further evidence of the strong Coastal Plain floristic affinities of these areas (see Carr and Kral). The label of *Channell & Rock 79* (GH), from Bladen County, North Carolina, notes that monarch butterflies (*Danaus plexippus*) abundantly visit the flowers of this species.

According to Millspaugh, some American Indians, particularly the Seminoles, made an invigorating tonic from the roots of *Lachnanthes caroliana*. They also prepared a tincture used for treating a variety of maladies. Millspaugh gives directions for making a whole-plant infusion and records a number of physiological reactions that it produces.

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2. **Lophiola** Ker-Gawler, Bot. Mag. **39:** *pl. 1596*. 1813.

Slender, perennial, stoloniferous herbs with erect, leafy stems from rhizomes; roots and rhizomes brown to whitish. Upper portions of stem, inflorescence branches, and outer portions of flowers densely woolly-tomentose with whitish, soft, contorted trichomes. Leaves basal and cauline, erect, linear, flattened, becoming progressively smaller above. Inflorescence a much-branched, many-flowered, bracteate, open [or compact] corymb terminating the erect stem and exceeding the leaves. Flowers regularly symmetrical, the insertion of the tepals and stamens perigynous. Tepals 6 in 2 whorls of 3, nearly equal, free to level of insertion, reflexed at anthesis, brownish or maroon at the tips, with a bright yellow crest of moniliform trichomes on the lower half of the adaxial surface, densely tomentose abaxially, inserted about the middle [or toward the base] of the ovary, persistent and erect in fruit, each whorl valvate in aestivation, with the outer 3 partially enclosing the inner 3. Stamens 6, erect-spreading at anthesis, shorter than the tepals; filaments glabrous, persistent, inserted opposite the tepals on the ovary; anthers yellow, introrse, basifixed, scarcely auriculate at the base. Ovary half-inferior [or nearly superior], 1-locular with 3 parietal placentae above and 3-locular with axile placentae below; style 1, terminal on the ovary, slender, about equalling the stamens, persistent in fruit; stigmatic area slightly 3-lobed; ovules numerous in several vertical rows, evidently anatropous. Capsule ± globose or ovoid, the valves beaked by persistent style segments, the fruit enclosed before dehiscence by the persistent tepals. Seeds numerous, tiny, elongate, variously curved, whitish; seed coat finely open-reticulate. TYPE SPECIES: *L. aurea* Ker-Gawler. (Name from Greek *lophia*, a mane or crest, evidently in reference to the pubescence on the adaxial side of the tepals.) — **GOLDEN-CREST.**

FIGURE 2. **Lophiola.** a–p, *L. aurea*: a, habit, × 1/4; b–e, series of cross sections of leaf from base to tip to show folding and progressive fusion of adaxial surfaces (black area in vascular bundles represents xylem and white is phloem). all × 6; f, open flower — note crest of trichomes on upper surface of tepals, × 6; g, flower in vertical section, ovary half-inferior, placentation parietal above, axile below, × 6; h, moniliform trichome from crest of tepal, × 150; i, cross section of ovary at level of upper arrow in "g," triangles represent filaments, × 12; j, cross section of ovary at level of lower arrow in "g," × 12; k, anatropous ovule, × 25; l, fruit just beginning to dehisce, one tepal removed — note style separating into 3 parts, × 6; m, dehisced capsule, × 6; n, same, one valve removed, × 6; o, mature seed, × 25; p, seed in vertical section, oriented as seed in "o," endosperm even-stippled, embryo unshaded, × 25.

One (or more ?) species occurring disjunctly along the Atlantic Coastal Plain of North America in western Nova Scotia; in the pine barrens of New Jersey (and formerly Delaware); in southeastern North Carolina; in south-central Georgia; and from the panhandle of Florida to southern Mississippi. The genus apparently occurs infrequently within each of the geographical regions, although individual populations may be composed of many individuals and may cover large areas. Plants of the genus are nearly always found in bogs and low, wet areas in savannahs and pine barrens.

Lophiola has not been studied in detail morphologically, developmentally, anatomically, cytologically, or ecologically, and its reproductive biology is unknown. Because of this general lack of information, the taxonomy and familial affinities of the genus are uncertain (see family discussion).

Fernald (1921, pp. 162, 163, 243, 244) noted apparent differences in the habit, indumentum, leaf size, compactness of the inflorescences, number of flowers, level of insertion of the tepals on the ovary, fruit color, and shape of the base of the seeds that occur between plants from Nova Scotia, New Jersey, and the southeastern United States. He described the plants from Nova Scotia as a new species, *Lophiola septentrionalis*, applied the name *L. americana* (Pursh) Wood to the plants of New Jersey, and used the name *L. aurea* Ker-Gawler for the plants of North Carolina, Georgia, Florida, and Mississippi. However, herbarium specimens and observations on living plants in North Carolina suggest that at least some of this variation may be due to ecological conditions. It is also to be expected that widely disjunct populations, even of the same species, would differ somewhat from each other. Thus, until more detailed studies reveal information to the contrary, it seems best to recognize only one species of *Lophiola*.

There has been considerable debate about whether the name *Lophiola aurea* Ker-Gawler (Bot. Mag. *pl. 1596*) was published before or after *Conostylis americana* Pursh (Flora Americae Septentrionalis 1: 224), which is the basionym of *Lophiola americana* (Pursh) Wood (Class Book 697. 1861). It appears that Pursh's *Flora* could not have been published before the middle of December, 1813. Graustein relates that the printing of this work was scheduled to be completed during the week of December 7, 1813, and that Pursh presented a copy to the Linnean Society of London on December 21, 1813. The plate of *L. aurea* in the *Botanical Magazine* bears the date "1 Nov. 1813." Plates of this period were dated to comply with British print copyright acts. Stearn (1943b) says that "the dates on these prints were intended to be those of their first publishing. . . . and in the absence of evidence to the contrary, the dates engraved on its [the *Botanical Magazine's*] plates, though possibly not always correct to the exact day, must be accepted as correct as to the month." Thus it seems clear that *L. aurea* was published before *C. americana*. The citation in the *Botanical Magazine* of Pursh's name for this plant and the

exact page number of its description in Pursh's *Flora* can be attributed to the supposed availability of the proofs of the *Flora* to the editor of the *Botanical Magazine* (see Stearn, 1943a).

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COVER: A "mass collection" of leaves of *Sassafras albidum* (Nutt.) C. G. Nees, a handsome lauraceous tree of eastern North America and a probable Arcto-Tertiary relict, along with its two living congeners in eastern Asia. Its attractive small, yellow flowers are produced early in the spring as the leaves first unfold. The elliptic leaves, either entire, mitten-shaped, or 3-lobed at apex, become beautifully red-and-yellow colored in autumn. Although sassafras has long been thought to have medicinal properties, it is probably no more than a mild aromatic stimulant. A tea is made from the wood of sassafras roots; from its leaves, which contain ethereal oil and mucilage cells, gumbo filé, a powder used to give flavor and consistency to gumbo soup, is prepared.

Karen S. Veimure, whose original illustrations were used on the two preceding covers, also planned and executed this one, as well as the designs and devices in other parts of the Journal and on the offprint covers.

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ARTURO BURKART

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ARTURO BURKART;* A PERSONAL APPRECIATION

OTTO T. SOLBRIG

I FIRST MET Professor Arturo Burkart in 1951 when I visited the Instituto Botanico "Darwinion" on the outskirts of Buenos Aires to check the holdings there in the family Caprifoliaceae. I was then a sophomore in college and was somewhat awed by the atmosphere of the place, with its high cathedral-like halls where ghostly figures worked in dark corners over their microscopes. I was particularly awed by the tall, imposing figure of the Director. Nevertheless, he took a liking to me, and for the next four years I made the three-hour trip from La Plata, where I was studying, to San Isidro once a week to learn botany from Burkart. He put me to work, first writing labels, then identifying plants, and then working up a small group of grasses, all in the old-world tradition of training herbarium taxonomists in which he believed so strongly. Later, I took Burkart's course in Forage Plants at the Agricultural School of the University of La Plata. There I saw another facet of him in his great love for Argentina's rural sector and his unshakeable belief that the future of the country lay in developing its agriculture through advancements in science. Shortly before Burkart's death, the Organization of American States conferred on him its highest scientific award, the "Bernardo Houssay" prize, in recognition of his agronomic work with alfalfa.

What I remember most about Burkart are his tremendous erudition, his careful scholarship, and his unqualified love for plants. He used to say that there were no ugly or uninteresting plants, and for him there were none. His careful scholarship was legendary, and on the rare occasion when an error was found in one of his papers, it was commented upon in the Argentine botanical community as an event worthy of special notice.

Of German parentage, Burkart was born and raised in Argentina, and he combined a strong sense of patriotic love for the country of his birth with pride in the achievements of German culture. He spoke and wrote German fluently and contributed scientific and general articles to German magazines in Europe and Argentina, in addition to writing his vast

* 1906–1975.

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bibliography in Spanish. He was strongly influenced by the liberal tradition of the early 20th century. He never could accept the venality, corruption, and political oppression of the Perón dictatorship, and he never compromised his stand, even at the risk of losing his posts. On the other hand, he was not able to understand some of the new forces at work in Argentina, and this led him to take stands, particularly in his last years, against groups and individuals who were trying to reform the University in accordance with the precepts of our times.

Burkart was Professor of Botany at the University of Buenos Aires at the time of his death. Prior to that, he had served for 20 years as Professor of Forage Plants at the University of La Plata. However, the institution which had first call on his allegiance was the Instituto Darwinion. This institute had its start when the wealthy Argentine botanist Cristobal M. Hicken, upon his death, donated his books, his herbarium, and a small endowment to the Argentine Academy of Sciences. Burkart was named its first director in 1937 at only 30 years of age, and he served in that capacity until his death. During these years, with a minimal staff of three to five permanent members, he transformed the small herbarium and library with which he started into the best one in Argentina, and possibly the best in South America. The journal *Darwiniana* became the favorite outlet for Argentine botanists, and it set editorial standards for others to emulate.

All who knew Arturo Burkart will miss this honest and forthright man who loved his country, his family, and his Darwinion so much, but who above all else loved the *Scientia amabile*, as he liked to call his vocation.

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A MONOGRAPH OF THE GENUS PROSOPIS (LEGUMINOSAE SUBFAM. MIMOSOIDEAE)

ARTURO BURKART *

THIS MONOGRAPH of *Prosopis* is the result of prolonged herbarium and field studies made over a period of several years with the intention of completing an exhaustive treatment of an important but difficult genus. The monograph represents the completion on a world scale and a revision of my earlier paper "Materiales para una monografía del género *Prosopis* (Leguminosae)" (Darwiniana 4: 57–128. 1940), which found wide acceptance for its more natural definition of the species. For the Mexican-Texan area of the genus, the work by M. C. Johnston (Brittonia 14: 72–90. 1962) on sect. ALGAROBIA was very helpful. Encouragement to write this paper came from those botanists interested in a broad research project on *Prosopis* (Structure of Ecosystems Program of the US/IBP).

I am conscious that this is not a final treatment and that amendments may be necessary as the results of new research become available. However, workers in nontraditional fields of phytotaxonomy and biology need up-to-date systematic accounts of the plants which they study.

My visits to the principal botanical institutions of the United States in 1973 and 1975, after I had seen most Argentine herbaria, gave me the final opportunity to finish this paper. I have to acknowledge with gratitude the interest and help received from many colleagues and friends during this task. Professor Otto Solbrig (Gray Herbarium, Harvard University, Cambridge, Massachusetts), Dr. Beryl Simpson (U. S. National Herbarium, Smithsonian Institution, Washington, D. C.), Dr. Marshall C. Johnston (University of Texas, Austin), and Dr. Peter Raven (Missouri Botanical Garden, St. Louis, Missouri) have to be mentioned in this connection. My thanks are also extended to the staff of the journal of the Arnold Arboretum for valuable editorial work.

* Professor Arturo Burkart, whose extensive treatment of *Prosopis* we are publishing here, visited the Harvard University Herbaria in the spring of 1975. I had previously reviewed the paper in some detail and was able to discuss various matters of arrangement and style with him. He seemed happy that publication would be possible within a year and gave me permission to make any changes in the English that I thought were necessary. Aside from normal editorial alterations, I have made changes only where not to have done so would have left the meaning obscure.

Professor Burkart died only a few weeks after leaving Harvard. We are glad to be able to publish this paper, which embodies some of his great knowledge of and experience with the Leguminosae, a plant family he studied all his life and which he knew better than almost anyone else in the New World.

Arturo Burkart was a helpful colleague and a good friend for many years. His passing is a great loss to American botany. We hope he would have been pleased with this publication of his study of *Prosopis*, his favorite genus. B. G. Schubert.

GENERIC DIAGNOSIS

Prosopis Linnaeus emend. Burkart.

TYPE SPECIES: *Prosopis spicigera* Linnaeus, Mantissa Pl. 68. 1767; cf. A. Burkart, Darwiniana 4: 59, 61. 1940. Now a synonym of *P. cineraria* (L.) Druce.

Flowers small, actinomorphic, pentamerous, hermaphroditic; aestivation valvate; calyx campanulate; corolla with linear petals, these fused or more or less free, glabrous or pubescent, frequently villous or pilose inside toward the tip; androecium of 5 + 5 free stamens; anthers elliptic, dorsifixed, introrse, with an apical, pedicellate, globose or ovoid connectival gland; pollen grains simple, isopolar, tricolporate, subspheroidal to prolate, the exine pertectate, baculate, the sexine bigger than the nexine, the grains large or small; ovary stipitate, villous or sometimes glabrous. Anthesis apparently protogynous, the filiform style emerging from the flower bud before the stamens appear; flowers greenish-white, yellowish with age, seldom red; insect-pollinated.

Fruit a modified indehiscent legume called a drupaceous loment, linear, straight, falcate, annular to spirally coiled; mesocarp fleshy, sugary or fibrous; endocarp divided into 1-seeded, coriaceous to bony segments, closed or sometimes opening easily, longitudinal or rarely biseriate and transverse; seeds ovoid, compressed, with fissural line on the faces (pleurogram), hard, brown, with mucilaginous endosperm (typical of Mimosoideae) surrounding the embryo; cotyledons flat, rounded, epigeous in germination.

Trees or shrubs of varying size, rarely subshrubs, predominantly xerophilous, aculeate, spiny or rarely unarmed. Leaves bipinnate, commonly with few pairs of opposite pinnae, only in a few subaphyllous species sometimes reduced, pinnate, paucifoliolate; petiole with circular, sessile, apical gland and sometimes smaller, similar ones on the rachis of the pinnae; leaflets small, numerous, mostly opposite, linear, oblong, fusiform, rarely large (*P. ruscifolia*), entire, of the same color on both sides; venation pinnate, not very prominent.

Racemes spikelike, amentiform, axillary, mostly densiflorous, sometimes with globose heads.

Shoots in most species dimorphic; megablasts long, flexuous, knotty in age; brachyblasts or short shoots emerging from multiple axillary buds (which develop the cauline spines when extant), leaf fascicles, and racemes.

CHROMOSOMES. The *Prosopis* species are mainly, if not entirely, diploid, with the somatic number of $2n = 28$. Polysomaty in root tips (cortical cells) is frequent and probably responsible for false tetraploidy interpretations, e.g., in *P. juliflora*. A supposedly tetraploid species from the Pacific Islands, *P. insularum* (Guill.) Breteler does not belong to the genus, but to *Schleinitzia* Warburg. Chromosomes in *Prosopis* are small

and uniform, without special distinctive marks. Meiosis seems to be normal even in supposedly hybrid populations.

DISTRIBUTION. About forty-four species distributed in Southwest Asia, Africa, and predominantly America, from western North America to Patagonia, mainly in warm and dry regions of the West, with the center of polymorphism in Argentina. Some species are cultivated and naturalized outside their original homes.

ECOLOGICAL AND ECONOMIC IMPORTANCE. Because of their abundance and ecological behavior, the *Prosopis* species are important vegetation elements in arid and semiarid countries, where many of them offer shade, firewood, timber, and food for man and shade and forage for wildlife and domestic herbivores. Their importance for Indian cultures has been very great in the past and is still considerable, in spite of much devastation. Not to be neglected is the value of the flowers as bee pasture. The edible fruits of some species and varieties are used as food in the form of meal or fermented beverages; however, these products have not yet gained general acceptance.

Some species, especially the mesquite (*P. glandulosa*) in Texas and the vinal (*P. ruscifolia*) in the Chaco, because of their tremendous invading power, have become nuisances to ranchers and are fought with all kinds of herbicides. Other species are planted for shade and forage in the tropics.

Ecologically, the legumes are important for the endozoic propagation of the hard seeds, which germinate freely after passing through the digestive tracts of cattle, sheep, goats, or wild animals such as the guanaco, the South American ostrich, the fox, etc. According to information given to me by O. T. Solbrig, not only are the fruits, if eaten, dispersed by the animals, but their passage through the digestive tract also benefits the seed by killing the Bruchid beetles (specialized legume predators) always present in *Prosopis* fruits. The nutritive legumes, with seeds resistant to the digestive juices of herbivores, demonstrate a superior adaptation of the species of *Prosopis* in their struggle for survival and dispersal.

There is a real need for more ecological studies on these species and for a selection program to aid forestation plans in arid and semiarid regions. Superior strains, especially of such useful species as *P. juliflora*, *P. chilensis*, *P. pallida*, *P. caldenia*, *P. alba*, *P. nigra*, *P. affinis*, *P. tamarugo*, etc. should be cultivated and tested at experiment stations of dry-climate countries in order to have them ready for large forestation programs.

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GENERIC LIMITS AND SUBDIVISIONS

Because of the uniformity of leaf, floral, and fruiting characters, there seems to be no reason for a subdivision of the genus such as was proposed by Britton and Rose (North American Flora 23: 180, 182–187. 1928) and followed in part by Hutchinson (1964).

The paribipinnate leaf, characteristic of the whole subfamily Mimosoideae, presents in most species of *Prosopis* only one or a few pairs of pinnae and never a solitary apical pinna, found, for instance, in the leaves

of *Caesalpinia* and *Hoffmanseggia* and other caesalpinioid genera, but entirely absent in the Mimosoideae.

Flowers in *Prosopis* are of the common actinomorphic, pentamerous, decandrous, hermaphroditic type, with gland-tipped anthers, apparently the primitive model of a mimosoid floret.

The fruit, a modified, indehiscent, more or less fleshy legume with the endocarp commonly hardened and segmented into one-seeded joints, is of a type which I have called "*lomento drupáceo*" (*lomentum drupaceum*; Burkart, Las Leguminosas Argentinas, sylvestres y cultivadas 21. 1943; *Ibid.* ed. 2. 17. 1952). In spite of the diversity of forms and curling, the fruit is fundamentally uniform, another sound reason for maintaining *Prosopis* sensu lato, essentially as it was established by G. Bentham. Too much weight has been given to the curvature and curling of the *Prosopis* fruit and its bearing on systematics. There is a parallel development in both main sections (STROMBOCARPA and ALGAROBIA), with variation from nearly straight to curved and spirally coiled loments. Only one difference exists; the closed corkscrew type is reached by only some members of sect. STROMBOCARPA, while in sect. ALGAROBIA the spirals are always fewer, larger, and open. This difference is of importance at the specific level.

In contrast with this uniformity of the fruit, there is a marked vegetative diversification in the armature, whether it consists of spines or prickles or is absent. These differences provide the best foundations for a sectional subdivision of the genus. Most authors of local treatments of *Prosopis* fail to recognize the importance of these differences of subgeneric rank, although I devoted a special paper to them (Burkart, 1937). Britton and Rose, for example (*loc. cit.*), made no distinction between "stipular spines" or "spinescent stipules" in their "genera" *Sopropis*, *Strombocarpa*, and *Neltuma*. Relying on the differences of armature to provide the only strict differences between sections, we may trace the following scheme, which notwithstanding its morphological nature possibly has phylogenetic significance:

1. Primarily unarmed. African species. . . . . Sect. ANONYCHIUM (species 4).
2. With cauline prickles (internodal hard emergences like the aculei of *Rosa* and *Rubus*). Asiatic and North African species. . . . . Sect. PROSOPIS (formerly sect. *Adenopis*) (species 1–3).
3. With stipular (foliar) spines; stipules very early in ontogeny developed into straight, paired spines. American species. . . . . Sect. STROMBOCARPA (including "*Sopropis*") (species 5–13).
4. With cauline, axillary, solitary or paired, multi- or uninodal, straight spines. American species.
   a) Spines axillary; shoots differentiated into macroblasts and knotty brachyblasts. Fruit compressed. . . . . Sect. ALGAROBIA (syn. *Neltuma*), *pro parte maxima* (species 15–44).
   b) Spines axillary and apical, uninodal, solitary; no brachyblasts. Fruit moniliform. . . . . Sect. MONILICARPA (species 14).
5. Secondarily unarmed, because of suppression of the axillary, cauline spines. American species, especially from Paraguay and Argentina. . . . . Sect. ALGAROBIA, *pro parte minima* (species 18, 20, 29, 35, 39, etc.).

The term "stipular spines" is ambiguous if not clearly defined. It may mean spinescent stipules, as in sect. STROMBOCARPA, or it may mean geminate, axillary, uninodal, cauline spines developed near the stipules but independent from them, as in sect. ALGAROBIA.

It is interesting to look at another large genus of the Mimosoideae, *Acacia*, to find a similar differentiation. The *Acacia* section or subgenus (Gummiferae Bentham) has spinescent stipules, just as does sect. STROMBOCARPA. *Acacia* subg. ACULEIFERUM Vassal (ser. Vulgares Bentham) has the internodal prickles of *Prosopis* sect. PROSOPIS (although mostly recurved prickles). Then there is one rare *Acacia* species in Australia, *A. pulchella* R. Brown, which has developed primitive, axillary, cauline, uni- or plurinodal, sometimes foliate spines and represents the morphological type of *Prosopis* sect. ALGAROBIA very weakly expressed. The extraordinary leaf polymorphism of the phyllodial acacias in Australia (ser. Phyllodineae Bentham) is not paralleled in *Prosopis*, in which no phyllodes are known. Instead, some species (sect. ALGAROBIA, ser. Sericanthae Burkart) are aphyllous or subaphyllous (leaves small and shed very early in the season), with photosynthesis being accomplished within the cortical tissue of branchlets and spines. This vegetative type is in turn very rare in the genus *Acacia*, although present in a few Australian species.

In other families as well, vegetative differences are also considered to be of infrageneric rank. See, for example, the recent reduction of *Junellia* Moldenke (Verbenaceae) to a section of *Verbena* by N. S. Troncoso (Darwiniana **18**: 312. 1974).

There is a floral character which could be considered as important. In sect. ANONYCHIUM, in its only species (and also the only tropical African one), *P. africana* (Guill., Perr., & Rich.) Taubert, the connective of the anther is broadened and the apical gland incurved together with it. This is beautifully portrayed in a recent plate of P. Brenan (in Hubbard & Milne-Redhead, Flora Trop. East Africa 35. London. 1959). At first I thought to use this character as one of sectional value, but later I was able to observe a somewhat similar incurving of the anther gland in *P. farcta* Solander ex Russell) Macbride of sect. PROSOPIS. This fact convinced me again of the generic unity of *Prosopis* in its wider delimitation.

Vegetatively, there is a great diversity in habit. One Oriental species, *P. farcta*, is known by its invading rootsuckers (or rhizomes?), by which it approaches the American *P. strombulifera* (Lam.) Bentham and its relatives. In this and some other characters, sect. STROMBOCARPA comes closer to sect. PROSOPIS than to the entire sect. ALGAROBIA, in which rhizomes or rootsuckers are unknown. However, there remains the basic difference between the two, prickles *versus* spiny stipules.

In sect. PROSOPIS one species, *P. cineraria* (L.) Druce, has longitudinal seeds, another, *P. farcta*, transverse seeds and segments in the fruit. This is a difference to which the rank of series is given in sect. STROMBOCARPA. However, in sect. PROSOPIS the discovery of the new *P. koelziana* Burkart, with its intermediate fruit fabric, reduces the systematic value of this

difference so that no series are distinguished. It is even less possible to revive *Lagonychium* M. Bieb. as a genus for *P. farcta*, as proposed by Bobrov in Komarov's *Flora of the USSR*.

PROBABLE EVOLUTIONARY DEVELOPMENT OF SPECIATION

Prosopis is a rather primitive genus within the Mimosoideae, as the simple pollen grains, the mostly free petals, and the decandrous condition prove. It possibly originated in tropical Africa, where only *P. africana*, the least specialized species, persists. Near relatives are *Adenanthera* L. and *Pseudoprosopis* Harms, with dehiscent legumes. From this or a similar ancestral stock may have evolved the more specialized groups, which have fleshy, indehiscent drupaceous legumes, nearly all with the vegetatively differentiated megablasts and/or brachyblasts (these are absent only in *P. argentina*, aside from in *P. africana*), and with pungent organs (also absent in *P. africana*). The prickly Asian species of sect. PROSOPIS developed in the eastern, arid desert zones. The spiny American ones developed in the western hemisphere into two sharply differentiated, parallel groups, also with desert climate preferences: sect. STROMBOCARPA (with spiny stipules) and sect. ALGAROBIA (with cauline, mostly axillary thorns). In between the two appeared the small section MONILICARPA, with only one isolated member, *P. argentina*, of doubtful origin and affinities. The related genus *Prosopidastrum* Burkart (formerly considered a section of *Prosopis*), with two species, one in Baja California and the other in Patagonia, is a side-branch, which seems to confirm a common origin in one ancient desert floral center. According to the Wegener theory of continental drift, land connections between east and west were easier at the end of the Mesozoic or the beginnings of Tertiary times, when these plant groups must have originated; so the ancestors of present-day *Prosopis* species may have migrated widely from the African center to both east and west, slowly evolving different species that were adapted not to long-distance dispersal, but to a very effective endozoic diffusion through mammals and larger birds (owing to the succulent, edible legumes with hard seeds that escape digestion). Present distribution patterns of species of *Prosopis* do not exclude the possibility of an ancient desert flora common to both Americas which later divided and became widely separated into two centers, the Mexican-Texan center and the Argentine-Paraguayan-Chilean one, where most species occur. The fact that in both centers endemic species exist indicates their antiquity and suggests that long-distance dispersal did play only a secondary role, if any. After millions of years, the speciation process (mainly gene mutations, as suggested by the karyogram uniformity) slowly originated the 40 American species and several varieties now known. Several facts indicate that in America the principal center of origin is Argentina and that the Mexican center is a secondary one. Or perhaps they are of the same age, but some factors, e.g., stronger competition with the boreal floras, prevented a major species development in that northern area of the genus.

TAXONOMIC HISTORY OF THE GENUS

The name *Prosopis*, selected by Linnaeus for this genus, is of ancient Greek origin and means a kind of prickly fruit, such as the head of *Arctium lappa* L. (Compositae). Pfeiffer (Nomencl. Bot. 2(2): 842. 1874) wrote, "Nomen ex Dioscoride, ubi Lappam significat." The interpretation of classic *Prosopis* as a species of *Petasites* (Dictionary of Gardening, Roy. Hort. Soc., Oxford, 1965) is incorrect. Linnaeus, in this case as in others, proceeded arbitrarily, changing a name of age-old tradition and raising the opposition of contemporary, erudite botanists such as Albrecht von Haller. However, at present Linnaeus's name must be accepted. He apparently knew only one species, the type species of *Prosopis* from the Near East, which he called *P. spicigera* in his *Mantissa Plantarum*, published in 1767.

Ludwig Pfeiffer, in his important bibliographic work mentioned above, offers a number of references to the early use of the name since Linnaeus, which I shall not repeat here. However, some of them are of value as milestones in the development of the taxonomy of *Prosopis*.

The *Ceratonia chilensis* of Ignacio Molina (Saggio sulla storia naturale del Chili 172. Bologna. 1782) seems to be the second species described. However, it was ignored for a long time, owing to its inclusion in the wrong genus; its author was misled by the similar Spanish name, structure, and uses of the fleshy legume of the Mediterranean St. John's bread, *Ceratonia siliqua* L. It is *Prosopis chilensis*, the "Algarrobo de Chile" (a big tree of the affinity of *Prosopis juliflora* (Sw.) DC. of northern South America and now the type of ser. Chilenses, ser. nov.) which causes taxonomists so much difficulty.

Mimosa juliflora of Olof Swartz, published in 1788, was the third species recognized, but it was not incorporated into *Prosopis* until 1825. *Mimosa strumbulifera* Lamarck (later corrected to *strombulifera*), Encycl. Méth. Bot. 1: 15, appeared in 1789 and was the first known species of sect. STROMBOCARPA. Willdenow transferred this to *Acacia* (Sp. Pl. ed. 4. 4(2): 1055. 1806).

The voyage of Humboldt and Bonpland to tropical America (1799–1805) contributed various species, first described as species of *Acacia* by Willdenow (*Ibid.* 1058, 1059) and later placed in the proper genus by C. S. Kunth (H.B.K. Nov. Gen. Sp. Pl. folio ed. 6: 305–310. 1823).

The founders of the present limits and subdivisions of the genus are A. P. De Candolle and G. Bentham, the universally known great plant systematists of the 19th century. The former (DC. Prodr. 2: 446 *et passim.* 1825) incorporated the American sect. ALGAROBIA (with the erroneous character "antherae eglandulosae"), enumerating 13 species, if we include the dubious *Prosopis affinis* Sprengel (evidently of this section but listed by De Candolle under species "non satis notae." De Candolle failed to incorporate *Lagonychium* M. Bieb., which is very near sect. ADENOPIS DC., the typical section of *Prosopis*, and he did not recognize sect. STROM-

BOCARPA, defined later by Bentham, in spite of his knowledge of two of its species, *P. torquata* (Lag.) DC. (*loc. cit.* 448) and "*Mimosa*" *strombulifera* Lam. (cited as *Acacia strumbulifera* (Lam.) Willd. in DC. Prodr. 2: 455).

Discrepancies concerning the generic limits of *Prosopis* continued for a time. C. S. Rafinesque Schmaltz, working quite independently and getting no acceptance for his views, founded the genus *Neltuma* Raf. (Sylva Telluriana 119. 1838), with *N. juliflora* as the type. Only a year later, Bentham considered *Prosopis* sect. ALGAROBIA DC. worthy of generic rank (*Algarobia* Bentham, Plantae Hartwegianae 13. 1839), but on false assumptions derived from De Candolle's partially incorrect description. Unfortunately, *Algarobia* is a synonym of *Neltuma* Raf. However, Bentham confirmed De Candolle's diagnosis of the spines, "spec. Americanae spinis nullis aut axillaribus" (Prodr. 2: 446. 1825), of utmost importance in the distinction of sections, stating (*loc. cit.*), "spinae axillares supra stipulas natae ut DC. l. c. in char. sectionis, nec stipulares ut in diagnosibus specificis."

A short time later, Bentham changed his mind and accepted *Prosopis* nearly in its present wider limits (Hooker's Jour. Bot. 4: 346–352. 1842). He maintained his system in the "Revision of the Suborder Mimoseae" (Trans. Linn. Soc. London 30: 376–381. 1875) and was followed by many authors, e.g., P. Taubert (in Engler & Prantl, Nat. Pflanzenfam. 3(3): 118, 119, 385. 1891).

In my paper "Materiales para una monografía del género *Prosopis* (Leguminosae)" (Darwiniana 4: 59, 60. 1940), I accepted and commented upon Bentham's system. In a previous paper on the morphology and ethology of the genus (Darwiniana 3: 24–47. 1937), I tried to give a sound morphological and anatomical basis for the distinction of spines in sects. ALGAROBIA and STROMBOCARPA.

The strongest attack against a wide concept of the genus came in modern times from Britton and Rose in their treatment of "Mimosaceae" (in North American Flora 23(3): 180, 182–187. 1928), followed later by a number of other authors not specialists in the study of Leguminosae. Britton and Rose recognized three genera, *Sopropis*, *Strombocarpa*, and *Neltuma* (*Algarobia*), describing at the same time nine new "species" of *Neltuma*, most of which have since fallen into synonymy. *Sopropis* Britton & Rose (as gen. nov.) is only an outstanding form of *Strombocarpa*. I explain elsewhere in the present paper my opinion that the main differences between sections PROSOPIS, ALGAROBIA, and STROMBOCARPA are the vegetative spine characters and are, therefore, only of subgeneric rank.

Those who prefer to divide the genus (an opinion which I do not sustain) must remember that the section STROMBOCARPA as a genus (*Strombocarpa* Englm. & A. Gray, Boston Jour. Nat. Hist. 5: 243. 1845) is antedated by *Spirolobium* D'Orbigny (Sertum Patagonicum. *tab. 13.* 1839) and sect. ALGAROBIA as a genus (*Algarobia* (DC.) Bentham, Plantae Hartwegianae 13. 1839) by *Neltuma* Raf. (Sylva Telluriana 119. 1838). In this case, *Prosopis* would be reduced to the three Asiatic species

known at present, and all the American ones would become either *Spirolobium* or *Neltuma*. The remaining African section, with only *P. africana*, would also have to be raised to generic rank, because it shows no affinity with the bulk of the American species, nor with the type section of *Prosopis*. This would cause a total change in the nomenclature of many well-known species, with no benefit to anyone. More modern approaches, from the karyological, palynological, and chemotaxonomic researches, do not support (or only slightly support) such a radical subdivision into four genera. Moreover, other large genera of the Mimosoideae, especially *Acacia*, would have to be divided on the same grounds of purely vegetative characters. Finally, why do we have the categories of subgenus, section, and series if we do not use them? These are of great help in expressing intrageneric affinities without the excessive splitting and resulting changes of names so often resisted by those who must use them. I follow here the principles of the *International Code of Botanical Nomenclature*.

Minor changes at the sectional level merit a brief consideration. Bentham, in his famous joint work with Hooker, *Genera Plantarum* (1(2): 591. 1865), defined a section CIRCINARIA with one tropical African species, which he later ("Revision of the suborder Mimoseae," Trans. Linn. Soc. London 30: 515. 1875) reduced to the synonymy of *Acacia albida* Delile. The species was called *P.? kirkii* by Oliver (Fl. Trop. Africa 2: 332. 1871). Such errors concerning the genus are not uncommon in dealing with tropical Mimosoideae when the specimens lack flowers, owing to a certain degree of convergence in the legume characters. Taubert, writing the treatment of the Leguminosae for Engler and Prantl's *Natürlichen Pflanzenfamilien*, accepted sect. CIRCINARIA in the text, but suppressed it in the *errata* section (3(3): 119, 385. 1891).

Another "section" which later had to be suppressed is sect. LOMENTARIA C. Spegazzini (Anal. Soc. Ci. Arg. 47: 286. 1899), based on *Prosopis striata* Bentham, a synonym of *Prosopis globosa* Gillies ex Hooker & Arnott. In a note I tried to clear up the bewildering synonymy of this Patagonian species (Burkart, Physis 20: 53, 54. 1945) without changing its position in sect. LOMENTARIA (Darwiniana 4: 63. 1940). However, the question of the correct genus was raised after the discovery by Dressler of a closely related taxon, *Prosopis globosa* var. *mexicana* Dressler, in Baja California, Mexico. This was later given specific rank, in a new genus, *Prosopidastrum* Burkart (Darwiniana 13: 436–443. 1964), with two species, *P. mexicanum* (Dressler) Burkart (the type) and *P. globosum* (Gillies ex Hooker & Arnott) Burkart. This is a remarkable instance of bicentrism — two very closely related species, one in northwestern Mexico, the other in Patagonia, with no other affinities. The genus *Prosopidastrum* has dehiscent legumes in the type species, but not in the other one; the two species are similar vegetatively, with stipules spiny and recurved and twigs ending in a spine, a combination not found in any *Prosopis*.

A NEW SYNOPSIS OF THE GENUS PROSOPIS
(With Descriptions of the Sections and Series)

Prosopis Linnaeus emend. Burkart.

Type species. *Prosopis spicigera* Linnaeus, Mantissa Pl. 68. 1767; cf. Burkart, Darwiniana 4: 59, 61. 1940. Now a synonym of *P. cineraria* (L.) Druce.

I. **Prosopis** sect. **Prosopis.**

Prosopis sect. *Adenopis* DC. Prodr. 2: 446. 1825.
Lagonychium M. Bieb. Suppl. Fl. Taur. Cauc. 3: 288. 1819.

Shrubs or small trees armed with internodal, straight prickles; no stipular or axillary spines. Flowers in spikelike racemes; petals and ovary entirely glabrous; pollen with areolate exine. Fruit slender or turgid, long or short, very slightly curved; seeds longitudinal or transverse.

Type species. The same as for the genus: *Prosopis cineraria* (L.) Druce.

Distribution. Southwest Asia, North Africa; three species.

II. **Prosopis** sect. **Anonychium** Bentham in Hooker's Jour. Bot. 4: 347. 1842; sect. "*Anonychia*" Bentham, "Revision of the Suborder Mimoseae," Trans. Linn. Soc. London 30: 377. 1875.

Unarmed trees. Leaves well developed; racemes spikelike. Petals glabrous; ovary and style hairy; anther gland introrse, on an expanded, incurved connective; pollen small, the exine perforated, with costae. Legume subterete, straight, thick; seeds longitudinal.

Type species. *Prosopis oblonga* Bentham, *loc. cit.*, a synonym of *P. africana* (Guill., Perr., & Rich.) Taubert.

Distribution. Tropical Africa; only one species.

III. **Prosopis** sect. **Strombocarpa** Bentham in Hooker's Jour. Bot. 4: 351. 1842.

Spirolobium D'Orbigny, Sertum Patagonicum. *tab. 13.* 1839.
Strombocarpa Engelm. & A. Gray, Boston Jour. Nat. Hist. 5: 243. 1845. according to Hutchinson, Gen. Fl. Pl. 1: 287. 1964.

Always spiny shrubs or trees, the spines foliar; stipules lignified, developed into paired, straight, divergent spines of variable length, mostly fused at base and somewhat decurrent from the nodes, external to the

axillary buds or foliate brachyblasts. Flowers in globose to ovoid heads or in more or less elongated spikes; corolla gamopetalous, the petals villous to scarcely pilose within at the tip; pollen medium-sized, the exine thick, ornamented. Leaves with only one pair of pinnae. Fruit straight, curved, or coiled into a dense spiral.

TYPE SPECIES. *Prosopis strombulifera* (Lam.) Bentham.

In this section two series can be distinguished.

Prosopis ser. **Strombocarpae** A. Burkart, ser. nov.

Endocarpii segmenta seminaque longitudinaliter disposita. Legumen rectum, falcatum, vel lateraliter in spiram tortum.

TYPE SPECIES. The same as for the section: *Prosopis strombulifera* (Lam.) Bentham.

DISTRIBUTION. Southwestern United States and Mexico to Chile and Argentina; seven species.

Prosopis ser. **Cavenicarpae** (Burkart) Burkart, comb. nov. BASIONYM: *Prosopis* sect. *Cavenicarpa* Burkart, Darwiniana **4**: 76. 1940.

Endocarpii segmenta seminaque in legumine transverse bifariam disposita. Legumen subrectum, falcatum, vel annulare, turgidum, haud lateraliter tortum.

TYPE SPECIES. *Prosopis ferox* Grisebach.

DISTRIBUTION. South America; two species.

IV. **Prosopis** sect. **Monilicarpa** Ruiz Leal ex Burkart, sect. nov.

Prosopis sect. *Monilicarpa* Ruiz Leal *nomen nudum* in Cohen, Cei, & Roig, Rev. Fac. Ci. Agr. Univ. Nac. Cuyo **13**: 31. 1968.

Frutices ramis teretibus elongatis flexuosis, foliis alternis haud fasciculatis, unijugis; spinae solitariae, axillares, breves, uninodales necnon apicales. Racemi laxi, elongati, pauciflori. Flores pro rata magni, pubescentes; petala intus pilosa; glandula antherali minima. Legumen drupaceum, moniliforme, elongatum, rubrum; articuli ovoideo-globosi haud compressi, isthmi valde constricti; endocarpium osseum.

TYPE SPECIES. *Prosopis argentina* Burkart.

DISTRIBUTION. Western Argentina; one species.

V. Prosopis sect. Algarobia DC. Prodr. 2: 446. 1825.

Neltuma Raf. Sylva Telluriana 119. 1838.
Algarobia (DC.) Bentham, Plantae Hartwegianae 13. 1839.

Trees, shrubs, or rarely subshrubs without rhizomes, spiny or rarely unarmed; spines cauline, axillary, uninodal, rarely multinodal, solitary or frequently paired and internal in position between the multiple buds and the main internode; stipules small, never spinescent. Flowers in spike-like racemes; petals more or less free, villous inside toward the apex; pollen small, the exine thin, slightly or not at all ornamented. Fruit a drupaceous legume, straight, falcate, annular, or coiled into a very lax and open spiral with 1 to 3 turns, stipitate and acuminate; seeds more or less numerous within, with hard or coriaceous endocarp segments in one longitudinal row.

TYPE SPECIES. *Prosopis juliflora* (Sw.) DC.

DISTRIBUTION. Warmer and drier parts of America; about twenty-nine species.

In this, the largest section, several series can be distinguished.

Prosopis ser. Sericanthae Burkart, ser. nov.

Frutices vel arbores subaphyllae, horridae, ramosae; rami spinosi, axillares et terminales, spinas multinodales formantes.

TYPE SPECIES. *Prosopis sericantha* Gillies ex Hooker & Arnott.

DISTRIBUTION. Argentina, Paraguay; two species.

Prosopis ser. Ruscifoliae Burkart, ser. nov.

Arbores foliatae; spinae axillares, uninodales, validae, parvae vel nullae, solitariae vel interdum alternatim 1 vel 2. Folia unijuga; foliola saepe pro genere magna vel mediocria, illis serierum sequentium maiores; racemi spiciformes. Legumen elongatum, compressum, articulis subquadratis.

TYPE SPECIES. *Prosopis ruscifolia* Grisebach.

DISTRIBUTION. Gran Chaco (Argentina, Paraguay); four species.

Prosopis ser. Denudantes Burkart, ser. nov.

Frutices ramosi, spinosi; spinae axillares, uninodales, semper solitariae. Folia parva vel mediocria, bipinnatim unijuga, caduca. Flores breviter racemosae. Legumen drupaceum, crassiusculum complanatumve, rectum vel incurvatum, subsiccum.

TYPE SPECIES. *Prosopis denudans* Bentham.

DISTRIBUTION. Southwestern Argentina (Patagonia, Cuyo); four species.

Prosopis ser. **Humiles** Burkart, ser. nov.

Frutices vel subfrutices spinosi, ramis (in sicco) striatis. Folia parva, bipinnatim unijuga vel reducta 2-foliolata, caduca. Spinae axillares, geminatae, uninodales, in sicco striatae. Racemi spiciformes, breves. Legumen compressum.

TYPE SPECIES. *Prosopis humilis* Gillies ex Hooker & Arnott.

DISTRIBUTION. Central Argentina, Paraguay; two species.

Prosopis ser. **Pallidae** Burkart, ser. nov.

Arbores vel frutices elati vel nani; spinae uninodales, axillares geminatae. Folia parva vel mediocria, contracta bipinnatim, pauci- vel plurijuga. Racemi elongati, foliis longiores vel subaequales. Legumen compressum, elongatum, subrectum vel annulare; segmenta endocarpi subquadrata vel elliptica, longitudinalia.

TYPE SPECIES. *Prosopis pallida* (Willd.) HBK.

DISTRIBUTION. Argentina to Mexico; seven species.

Prosopis ser. **Chilenses** Burkart, ser. nov.

Arbores vel frutices; spinae uninodales, axillares, geminatae, validae vel parvae, interdum nullae, rarius alternatim 1 vel 2 pro nodo in eodem ramulo. Folia bipinnata pauci-(1–4-)juga, saepe ampla; racemi spiciformes foliis aequilongae vel breviores aut paullo longiores; foliola parva, mediocria usque longiuscule lineares, in rachide approximata vel dissita. Legumen drupaceum elongatum, plus minusve pulposum, lineare, compressum, subrectum, falcatum, annulare vel laxe spiraliter tortum; segmenta endocarpii numerosa, uniseriata, coriacea, saepe subquadrato-ovata, isthmi lati.

TYPE SPECIES. *Prosopis chilensis* (Molina) Stuntz emend. Burkart.

DISTRIBUTION. Southwestern United States and Mexico to Chile, Argentina, and Uruguay; eleven species.

SYSTEMATIC INDEX OF THE KNOWN SPECIES AND VARIETIES OF PROSOPIS

(Arranged by Sections and Series)

Prosopis Linnaeus emend. Burkart

I. *Prosopis* sect. Prosopis (syn. sect. *Adenopis*)

1. *P. cineraria*
2. *P. farcta*
   var. *farcta*
   var. *glabra*
3. *P. koelziana*

II. *Prosopis* sect. Anonychium

4. *P. africana*

III. *Prosopis* sect. Strombocarpa (syn. *Spirolobium*)

Ser. Strombocarpae
5. *P. strombulifera*
   var. *strombulifera*
   var. *ruiziana*
6. *P. reptans*
   var. *reptans*
   var. *cinerascens*
7. *P. abbreviata*
8. *P. torquata*
9. *P. pubescens*
10. *P. palmeri*
11. *P. burkartii*

Ser. Cavenicarpae
12. *P. ferox*
13. *P. tamarugo*

IV. *Prosopis* sect. Monilicarpa

14. *P. argentina*

V. *Prosopis* sect. Algarobia (syn. *Neltuma*, *Algarobia*)

Ser. Sericanthae
15. *P. sericantha*
16. *P. kuntzei*

Ser. Ruscifoliae
17. *P. ruscifolia*
18. *P. fiebrigii*
19. *P. vinalillo*
20. *P. hassleri*
   var. *hassleri*
   var. *nigroides*

Ser. Denudantes
21. *P. denudans*
var. *denudans*
var. *patagonica*
var. *stenocarpa*
22. *P. ruizleali*
23. *P. castellanosii*
24. *P. calingastana*

Ser. Humiles
25. *P. humilis*
26. *P. rojasiana*

Ser. Pallidae
27. *P. rubriflora*
28. *P. campestris*
29. *P. pallida* (including *P. limensis*)
30. *P. affinis* (syn. *P. algarobilla*)
31. *P. articulata*
32. *P. elata*
33. *P. tamaulipana*

Ser. Chilenses
34. *P. chilensis*
var. *chilensis*
var. *riojana*
var. *catamarcana*
35. *P. juliflora*
var. *juliflora*
var. *inermis*
var. *horrida*
36. *P. nigra*
var. *nigra*
var. *ragonesei*
var. *longispina*
37. *P. caldenia*
38. *P. laevigata*
var. *laevigata*
var. *andicola*
39. *P. flexuosa*
forma *subinermis*
40. *P. glandulosa*
var. *glandulosa*
var. *torreyana*
var. *prostrata*
41. *P. alpataco*
42. *P. alba*
var. *alba*
var. *panta*
43. *P. velutina*
44. *P. pugionata*

1. Petals glabrous. Prickly or unarmed shrubs or trees; no stipular or axillary spines present. Flowers in elongate, spikelike racemes. Legume elongate, slender or thick, straight to subfalcate.
   2. Ovary glabrous. Shrubs or trees mostly armed with internodal, straight, divergent prickles. Stipules caducous, foliaceous, leafletlike or a little larger; leaflets small. Anther gland straight. (Sect. PROSOPIS.)
      3. Leaves 1–3-jugate, glabrous. Legume long-stipitate, the stipe 0.8–2 cm. long; fruit slender, somewhat moniliform, linear to much elongate, cuneate at base. Seed segments longitudinal to transverse.
         4. Legume very slender and elongate, cylindroid-subtorulose, 8–19 cm. long × 4–7 mm. in diameter. Seeds longitudinal, separated from each other, in one row. Spikelike racemes solitary or mostly paniculate; primary bract amplexicaul, with oblique insertion. Southwest Asia. ..... 1. *P. cineraria.*
         4. Legume short-linear, subtorulose, 4–6 cm. long × 8–10 mm. in diameter. Seeds approximated, in transverse-oblique position. Racemes solitary, axillary; bracts lacking. Iran. ..... 3. *P. koelziana.*
      3. Leaves 2–7-jugate, pubescent or glabrous. Legume short-stipitate, turgid, ovoid to thickly terete, rounded and longitudinally furrowed at base, straight or more often inwardly curved. Seeds transverse, in two rows. Racemes solitary, without basal amplexicaul bract. Southwest Asia. ..... 2. *P. farcta.*
   2. Ovary villous or hirtellous. Unarmed trees. Stipules small, not foliaceous; leaflets medium-sized, larger and fewer. Anther gland introrse, on a broad, inwardly curved connective. Legume straight, subterete, thick. (Sect. ANONYCHIUM.) Tropical West Africa to Ethiopia. ..... 4. *P. africana.*
1. Petals internally villous or at least somewhat pilose toward the apex, externally glabrous or pubescent. Ovary pubescent to villous. Trees, shrubs, or subshrubs armed with stipular or axillary spines, sometimes (secondarily) unarmed, never prickly. Flowers in spikelike racemes or heads. Legume elongate, subcylindric or more often compressed, straight, curved, or spirally coiled, rarely moniliform.
   5. Spines foliar; stipules transformed into straight, divergent, paired spines, small or large, but present on all nodes, mostly united at base and more or less decurrent, external in position to the axillary bud or brachyblast (short shoot). Leaves with only one pair of pinnae; leaflets small, numerous. Flowers in spikes or heads, reddish-yellow, corolla gamo- or dialypetalous. Legume straight, falcate, or coiled into an open or dense spiral. Endocarp segments longitudinal or transverse. (Sect. STROMBOCARPA.)
      6. Endocarp segments and seeds in longitudinal position, forming one row; segments developed and closed, or endocarp thin, nearly continuous. Fruits various, ranging from straight to laterally coiled like a corkscrew. Trees or shrubs. (Ser. Strombocarpae.)

7. Legume subterete, nearly straight to subfalcate. Flowers sessile, in spikes. Petals highly connate, nearly glabrous inside. Mexico, Baja California. ..... 10. *P. palmeri.*
7. Legume always laterally curled or coiled in more than 1 or 2 open or closed circles. Flowers in heads or spikes. Petals more or less free.
   8. Flowers in elongate spikes; floriferous rachis 2–8 cm. long.
      9. Legume moniliform, in a few (1–3) coils with a central hole. Endocarp segments bony. Small tree. Central and northwestern Argentina. ..... 8. *P. torquata.*
      9. Legume not or scarcely moniliform, in closed coils without central hole. Endocarp segments coriaceous to thin, delicate, often continuous.
         10. Coils of the legume few (1–3), irregular, submoniliform, several legumes together forming a globose mass. Large, dense shrub with spreading horizontal branches. Northern Chile: Tarapacá. 11. *P. burkartii.*
         10. Coils of the legume numerous, regular, the margins parallel, the spirals usually forming a cylindrical structure. Tree. Southwestern North America. ..... 9. *P. pubescens.*
   8. Flowers in short-cylindric, ovoid or globose heads; floriferous rachis 1 cm. or less long.
      11. Heads ovoid to short-cylindric, 1.5–1.8 cm. long. Legume reddish-brown, in 2 to 7.5 irregular, dense coils. Tall shrub or small tree. Central Argentina. ..... 7. *P. abbreviata.*
      11. Heads perfectly globose. Legume yellow, in more numerous, regular coils. Smaller shrubs forming loose thickets by creeping gemmiparous roots (or rhizomes?).
         12. Leaflets separated, glabrous, in 3 to 8 pairs per pinna. Western Argentina, northern Chile, Peru(?). ..... 5. *P. strombulifera.*
         12. Leaflets close together, mostly pubescent after drying imbricated, in (2 to) 6 to 12 pairs per pinna, smaller. ..... 6. *P. reptans.*
            13. Leaflets pubescent; bracts small. Central Argentina, Peru. ..... 6. *P. reptans* var. *reptans.*
            13. Leaflets glabrous or of a more villous type, especially when young; bracts larger and villous. Texas. ..... 6. *P. reptans* var. *cinerascens.*
6. Endocarp and seeds in transverse position, mostly alternate segments forming two rows. Fruits thicker, subcylindric, nearly straight, falcate or once-annular, ring-shaped, incurved, not laterally coiled. (Ser. Cavenicarpae.)
   14. Tree becoming 15–18 m. tall in age. Stipular spines 0.5–3.8 cm. long. Leaflets obtuse. Legume curved, forming a half to complete ring, subtorulose, 7–11 mm. in diameter, the sutures impressed. Seeds 3–4.3 mm. long. Northern Chile. ..... 13. *P. tamarugo.*
   14. Trees or shrubs 2–5 m. tall. Stipular spines up to 5 cm. long. Leaflets acute or mucronate. Legume straight or

incurved, not torulose, 10–18 mm. in diameter, 2.5–7 cm. long × 1–1.8 cm. thick; placental suture prominent. Seeds 4.5–6 mm. long. Extreme northwestern Argentina, southern Bolivia. ..... 12. *P. ferox.*

5. Spines cauline; thorns resulting from metamorphosed branchlets, multi- or uninodal, long or short, not on all nodes but seldom entirely absent, solitary or frequently in axillary pairs ("geminate"), then internal in position between the multiple buds (brachyblasts or short shoots) and the main branch internode. Leaves with one to 8 pairs of pinnae, sometimes reduced. Racemes spikelike (amentiform), slender; flowers yellowish or sometimes red, the petals little connected, more or less free. Fruit a drupaceous loment, linear, rarely moniliform, straight, falcate or in a few open coils. Endocarp articles longitudinal, in one row. (Sect. MONILICARPA and sect. ALGAROBIA.)
   15. Plants spiny; spines present on at least some nodes, generally better developed on strong shoots than on small twigs.
      16. Spines multinodal; terminal and lateral thorns, with scars representing the reduced leaves. Subaphyllous, horridulous shrubs or trees, with all branchlets spiny. Legume nearly straight or slightly curved, dark or dullish red. (Sect. ALGAROBIA, ser. Sericanthae.)
         17. Shrubs. Calyx and corolla hirtellous outside. Flowering racemes short, ovoid. Spiny twigs slender, ca. 0.8–2.5 mm. in diameter. Legume 7–14 cm. long × 0.8–1.3 cm. wide, somewhat constricted between the endocarp segments; exocarp dark, dullish red. Northwestern and west-central Argentina. .... 15. *P. sericantha.*
         17. Trees. Calyx and corolla glabrous outside. Flowering racemes slender, elongated. Spiny twigs thicker, ca. 1.2–5 mm. in diameter. Fruit larger, 10–17 cm. long × 1.5–2.6 cm. thick, not constricted, the exocarp nearly black at maturity. Paraguay, southeastern Bolivia, north-central Argentina (Gran Chaco region). ..... 16. *P. kuntzei.*
      16. Spines uninodal; thorns lateral or exceptionally so (*P. argentina*) and some terminal, without scars. Foliage well developed or some species subaphyllous. Fruits varied, yellowish to brown, red, or violet-spotted.
         18. Axillary spines solitary, only one per node, exceptionally solitary or geminate on the same twig. Leaves with one pair of pinnae, rarely bijugate.
            19. Spines axillary and some terminal, small. Branching uniform, with only megablasts (long shoots), but without brachyblasts (short axillary, knotty shoots). Flowers rather large; calyx and corolla pubescent outside. Legume moniliform; segments globose-ovoid, acute, thick, with thin isthmi; exocarp bright red, showy. Anther gland very small. (Sect. MONILICARPA.) Northwest Andean Argentina. ..... 14. *P. argentina.*
            19. Spines always axillary (or lateral). Branching double, with elongate megablasts forming the skeleton of the treetops and abbreviated axillary brachyblasts from multiple buds producing fascicles of smaller leaves and inflorescences. Corolla glabrous or pubescent outside; florets smaller. Legume linear-oblong,

compressed; endocarp segments flat, subquadrate to ellipsoid, with broad, rarely contracted isthmi; exocarp yellow, brown, or violet-spotted. Anther gland larger. (Sect. ALGAROBIA.)

20. Leaflets exceptionally large and broad, 2–10 cm. long × 0.7–3.8 cm. broad, only 2 to 5 pairs per pinna. Spines always solitary, large, up to 33 cm. long. Legume long, compressed, constricted between segments. Trees. (Ser. Ruscifoliae.) ..... 17. *P. ruscifolia.*

20. Leaflets smaller to very small, sometimes medium-sized, or if long, then linear, narrow.

21. Spines always solitary per axil. Leaflets small, 1.5–12 mm., exceptionally to 15 mm. long, alternate on lower part of pinna. Leaves small to medium-sized (*P. ruizleali*). Shrubs. Racemes medium to short. (Ser. Denudantes.) Argentine endemics: Cuyo and Patagonian provinces.

22. Racemes spikelike; flowers pedicellate. Leaflets distant on the rachis.

23. Twigs without prominent nerves, soon reddish-brown. Legume turgid, nearly black at maturity, glabrous. Leaves glabrous.

24. Leaves small, with 1 to 4 pairs of leaflets per pinna. Legume falcate to annular, sometimes straight or thin. Argentina: Patagonia. ..... 21. *P. denudans.*

24. Leaves larger, to 8–9 cm. long, with 3 to 9 pairs of leaflets per pinna. Legume thick, straight, falcate to subannular. Western Argentina: Mendoza and Neuquén. ..... 22. *P. ruizleali.*

23. Twigs longitudinally nerved, green for a longer period. Legume compressed, olive-brown, pubescent. Leaflets pubescent, 4 to 7 pairs per pinna. West-central Argentina: Prov. San Juan. ..... 24. *P. calingastana.*

22. Short, subglobose flower heads; florets sessile. Leaflets very small, approximate-imbricate, 1.6–3.5 mm. long, 3 to 12 pairs per pinna. Twigs greenish, with several longitudinal, prominent nerves. Legume broadly oblong, much flattened, somewhat curved; pericarp thin, dry; segments subquadrate. Western Argentina: Mendoza and Neuquén. ..... 23. *P. castellanosii.*

21. Spines solitary or geminate alternately along the branchlets, sometimes all solitary. Leaflets larger, medium-sized to long and narrow, mostly 15–63 mm. long, exceptionally only 8 mm. long, opposite on the pinnae. Leaves medium to rather large. Spikelike racemes cylindrical, long. **Trees or large shrubs.**

25. Legume not moniliform, its margins parallel or subparallel. Spines short.

26. Leaflets oblong, less than 5 times as long as broad, herbaceous, ca. 6–23 mm. long ×

1.6–5.5 mm. broad. Legume straight, falcate only at the apex, mostly straw-colored or brown. Trees or tall shrubs. Tropical coasts, Mexico, Central America, Antilles, northern South America. Also cultivated. (Ser. Chilenses.) ..... 35. *P. juliflora* var. *juliflora.*

26. Leaflets linear (except for abnormal, diseased(?) ones usual on the same twigs), more than 5 times longer than broad, subcoriaceous, ca. 0.7–63 mm. long × 1.5–4.5 mm. broad. Legume straight, brownish. Trees or shrubs, erect to prostrate. Southwestern North America. ..... 40. *P. glandulosa.*

25. Legume moniliform, slender, elongate, compressed, its margins undulate, faces spotted. Spines large, small, or absent. Leaflets tending to fusiform, 10–30 mm. long × 2–12 mm. broad. Argentina: Gran Chaco. (Ser. Ruscifoliae.) ..... 19. *P. vinalillo.**

18. Axillary spines geminate, nearly constantly two pairs of spines per node. Leaves with 1 to 8 pairs of pinnae, in most species ample, 1–3-jugate, in some reduced.

27. Leaves reduced, very small, deciduous, dominated by the well-developed, long spines. Subaphyllous glabrous shrubs or subshrubs. Twigs and spines longitudinally striate. Legume subfalcate, compressed. (Ser. Humiles.)

28. Subshrub with woody rootstocks; branchlets and spines prominently nerved and sulcate. Flowers bright red. Leaves 1-jugate, the leaflets 1 to 3 pairs per pinna, small, oval; or leaves simply pinnate, with 1 to 2 pairs of leaflets. Spikes frequently replacing one spine of a pair. Central Argentina. ..... 25. *P. humilis.*

28. Larger shrub or tree; branchlets and spines longer, less striate. Flowers dull in color. Leaves always bipinnate, 1-jugate; petiole dilated at summit; leaflets 8 to 17 pairs, small, imbricate. Paraguay: Chaco. ..... 26. *P. rojasiana.*

27. Leaves well developed or if small, never simply pinnate. Twigs and spines terete, neither nerved nor sulcate.

29. Pinnae 3 to 8, mostly 5 pairs per leaf. Stamens and styles bright red. Racemes long, slender, longer than the leaves; leaflets numerous, small, approximate. Medium-sized tree; spines small. Northeastern Paraguay. (Ser. Pallidae.) ..... 27. *P. rubriflora.*

29. Pinnae only 1 to 4 pairs per leaf. Flowers greenish-white to yellowish with age.

* See also species no. 20, *P. hassleri*, with small spines.

30. Dwarf, 10–50 cm. tall, prostrate, extended, much-branched, hard, thorny little shrub. Leaves small, with 1 to 2 pairs of pinnae, pubescent; leaflets 1.5–6 mm. long, linear, approximate, 6 to 17 pairs per pinna. Racemes ovoid-cylindric; flowers pubescent. (Ser. Pallidae.) Central Argentina: Córdoba mountains. ..... 28. *P. campestris.*

30. Larger shrubs or trees, mostly 1 m. to more than 15 m. tall. Pinnae 1 to 4 pairs.

31. Leaves small, contracted; racemes long, slender, longer than or equalling the leaves. Leaflets approximate, pubescent to glabrous or only ciliolate. (Ser. Pallidae and ser. Chilenses *pro parte.*)

32. Legume dry, compressed, its margins undulate, the pericarp thin; endocarp segments rhombic, with longitudinal or oblique seeds, the isthmi very narrow, central. Leaves 1(–2)-jugate; leaflets 6 to 20 pairs per pinna; pinnae 0.4–6.5 cm., shorter than or equalling the racemes. Northwestern Mexico. ..... 31. *P. articulata.*

32. Legume fleshy, compressed but thicker; endocarp segments ovate to subquadrate, the isthmi broad, nearly as broad as the segments. Leaves various.

33. Leaflets prominently pinnatinerved below; 6 to 30 pairs per pinna, broadly oblong, obtuse, 2–8.3 mm. long, more or less pubescent or ciliate. Legumes straight with parallel margins or little constricted.

34. Legumes broad, 0.9–1.6 cm. in diameter.

35. Leaflets obtuse or obtuse and mucronate, 6 to 15 pairs per pinna, 2.5–8.3 mm. long and 1.4–4 mm. broad. Spines small, sometimes absent. Legume straight, thick, straw-yellow, 1–1.5 cm. broad, glabrous. Southern Colombia to Peru; Hawaiian Islands. ..... 29. *P. pallida.*

35. Leaflets subacute or acute, 10 to 30 pairs per pinna, linear, 2–7.5 mm. long × 0.8–1.8 mm. broad. Spines small. Legume submoniliform, annular, spotted, glabrous, 0.9–1.6 cm. broad. Northeastern Argentina, Paraguay. ..... 30. *P. affinis.*

34. Legumes narrow, 0.6–0.8 cm. broad.

36. Spines strong, divergent horizontally, the internodes to 7.5 cm. long, often constricted at base. Foliage green. Legume straight, pubescent. Tall shrubby tree. Western Gran Chaco. ..... 32. *P. elata.*

36. Spines weak, never horizontally divergent. Foliage small, glaucous.

Legumes straight, glabrous or puberulous. Small trees. Mexico: Tamaulipas. ..... 33. *P. tamaulipana.*

33. Leaflets without nerves or only the midrib (costa) visible below. Leaves small, delicate; racemes longer. Large tree. Central Argentina. ..... 37. *P. caldenia.*

31. Leaves larger, ample, expanded, lax, equalling the racemes in length or a little longer or shorter. Leaflets numerous, distant or approximate on the rachis. Trees or shrubs.

37. Leaflets small, 2–7.5(–10) mm. long, linear-oblong, obtuse, approximate, overlapping, touching each other or separated by less than their own width; glabrous or rarely ciliolate. Trees or large shrubs. (Ser. Nigrae.)

38. Trees, becoming large in age, the tops round with pendulous twigs and neat trunk. Spines small, absent on small branchlets.

39. Leaflets pubescent, close together on the pinna. Mexico. .. 43. *P. velutina.*

39. Leaflets glabrous.

40. Leaflets oblong, reticulately pinnate-nerved below, 4–7 mm. long × 1.2 mm. broad, neither distant nor approximate, touching the rachis. Legume straight to subfalcate, compressed-moniliform. Central Argentina and the Gran Chaco. ..... 36. *P. nigra.*

40. Leaflets linear, smaller, without nerves or only the midrib (costa) visible below, 2.7–5.4 mm. long × 0.2–1.1 mm. broad, approximate. Legume falcate to coiled in 2 to 3 open, lax spirals, not moniliform. South-central Argentina. ..... 37. *P. caldenia.*

38. Large shrub. Spines large, directed horizontally, stout. Argentina: western Gran Chaco (see ser. Pallidae in key (31) above). ..... 32. *P. elata.*
With slender, long spines; trees. ..... 36. *P. nigra* var. *longispina.*

37. Leaflets (or at least most of them) larger, 4–63 mm. long. (Ser. Chilenses and a transitional species of ser. Ruscifoliae.)

41. Leaflets pubescent, medium-sized, 5–15(–20) mm. long. × 2–4.8 mm. broad. Pinnae 1 to 4 pairs.

42. Legume glabrous. Leaflets distant, 12 to 14 pairs per pinna, pubescent to subglabrous. Racemes 9–12 cm. long. Twigs soon blackish or gray. Northern Peru. ..... 35. *P. juliflora* var. *horrida.*

42. Legume velvety pubescent, mainly when unripe. Leaflets approximate, 12 to 30 pairs per pinna, pubescent. Racemes 5–10 cm. long. Twigs greenish-brown. Southwestern North America. ..... 43. *P. velutina*.

41. Leaflets glabrous or only ciliolate on the margins, medium-sized to large.

43. Leaflets large, 10–63 mm. long, glabrous, separated on the rachis by more than their own width.

44. Leaflets linear, narrow, or in some varieties broader, 1.1–5.4 cm. long × 1.1–3(–5) mm. broad; costa visible but of the same color as the mesophyll; secondary veins absent, obscure, or a few subparallel from base. Legume broad to narrow, straight, falcate, or annular according to varieties. Large trees or tall shrubs; spines always geminate, sometimes absent. Peru, Bolivia, central Chile, northwestern Argentina. ..... 34. *P. chilensis*.

44. Leaflets somewhat broader or veins more visible; costa light-colored, contrasting with the mesophyll. Spines alternately geminate or solitary on the same shoot. Legumes straight.

45. Leaflets lanceolate to elliptic-oblong or fusiform, 10–30 mm. long × 2–12 mm. broad. Legume slender, elongate, subfalcate or straight, compressed-moniliform. Tree. Argentina: Gran Chaco. ..... 19. *P. vinalillo*.

45. Leaflets linear to oblong-linear, 7–63 mm. long, distant, 5 to 15 times as long as broad. Usually shrubby. Legume thicker. North America: Texas, Mexico. ..... 40. *P. glandulosa*.

43. Leaflets medium-sized, ca. 4–23 mm. long, approximate or distant, glabrous or only ciliolate on margins.

46. Leaflets elliptic-oblong, broad, usually not separated by more than their own width.

47. Leaflets ca. 15 to 41 pairs per pinna, approximate, subcoriaceous, 5–15 mm. long, 2 to 7 times as long as broad. Legume straight, thick. Mexico. ..... 38. *P. laevigata*.

47. Leaflets less than 30 pairs per pinna, more distant.

48. Leaflets herbaceous, oblong, pinnatinerved, corrugated when dry, 6 to 15 pairs per pinna, 10–23 mm. long. Trees or tall shrubs; spines rather small, geminate or alternately solitary and paired. Legume elongate, subfalcate, yellow, with parallel margins. Tropical coasts, Antilles, northern South America, and Central America. ..... 35. *P. juliflora*.
48. Leaflets subcoriaceous, thicker, not becoming corrugated by dessication, distant on the rachis.
    49. Leaflets short, 4–12 mm. long. West-central Argentina. ..... 39. *P. flexuosa*.
    49. Leaflets longer, 15–25 mm. Mexico, southwestern United States. 40. *P. glandulosa* var. *torreyana*.

46. Leaflets very narrowly linear.
    50. Large trees. Leaflets numerous, 25–50 pairs per pinna, moderately separated or approximate, 5–17 mm. long × 1–2 mm. broad. Legume much compressed, yellow, falcate to annular; margins parallel; pulp sweet. Central and northwestern Argentina. 42. *P. alba*.
    50. Trees or shrubs. Leaflets less numerous and the pairs farther apart on the rachis; distance greater than the width of the leaflets.
        51. Tall (0.2–3 m.) shrub with thick underground horizontal branches and thin erect aerial shoots. Pinnae 1 to 2 pairs, 3–14 cm. long; leaflets 9 to 25 pairs, 5–17(–30) mm. long × 0.9–1.5 mm. broad. West-central Argentina. ..... 41. *P. alpataco*.
        51. Trees or tall shrubs with trunk, this sometimes short.
            52. Spines very long and strong. West-central Argentina. ..... 44. *P. pugionata*.
            52. Spines small or scarce. Western Argentina. ..... 39. *P. flexuosa*.

15. Plants unarmed; spines probably absent by reduction. Trees. (Various series of sect. ALGAROBIA.)
    53. Leaflets large, 0.8–6.5 cm. long. Branchlets reddish; leaves darkening when dry, 1-jugate.

54. Leaflets large, 2 to 9 pairs per pinna, 2.5–6.5 cm. long × 2–4 cm. broad, similar to those of *P. ruscifolia*, but more nearly ovate, obtuse, darkening when dry. Legume linear, compressed, yellow, its margins parallel. Paraguay; Argentina: Formosa (eastern Chaco). . . . . 18. *P. fiebrigii.*

54. Leaflets somewhat smaller, more nearly linear and more numerous, 6–26 pairs per pinna, 0.8–4 cm. long × 1.8–16 mm. broad, glaucous-reddish when dry. Legume similar. Paraguay; Argentina: eastern Formosa to northern Santa Fe. . . . . 20. *P. hassleri.*

53. Leaflets much smaller, ovate or linear. Branchlets not reddish.

55. Leaflets glabrous. Leaves 1–2-jugate.

56. Leaflets distant, 5–13 mm. long. Heartwood dark. Western Argentina. . . 39. *P. flexuosa* var. *subinermis.*

56. Leaflets approximate, shorter, 1.5–3.2 mm. long. Heartwood yellow. Argentina: Santa Fe. . . . . 36. *P. nigra* var. *ragonesei.*

55. Leaflets pubescent.

57. Racemes longer than the leaves. Leaflets 2.5–8.3 mm. long. Southern Colombia, Ecuador, northern Peru, Hawaiian Islands. . . . . 29. *P. pallida* forma *pallida.*

57. Racemes of nearly the same length as the leaves. Leaflets 6–20 mm. long. . . 35. *P. juliflora* var. *inermis.*

TABLE 1. The natural geographic areas of development of species of Prosopis.

AREA	TOTAL NO. OF SPECIES	SPECIES
SOUTHWEST ASIA AND NORTH AFRICA	3	*P. cineraria*; *P. farcta*; *P. koelziana.*
TROPICAL AFRICA	1	*P. africana.*
TEXAN-MEXICAN AREA	8	*P. pubescens*; *P. palmeri*; *P. articulata*; *P. tamaulipana*; *P. juliflora*; *P. laevigata*; *P. glandulosa*; *P. velutina.*
TROPICAL ANDEAN REGION (Colombia to the extreme north of Chile and northwest of Argentina)	6	*P. burkartii*; *P. ferox*; *P. tamarugo*; *P. pallida* (including *P. limensis*); *P. chilensis*; *P. juliflora.*
ARGENTINIAN-PARAGUAYAN CENTER AND NEIGHBORING AREAS		
GRAN CHACO AND ADJOINING AREAS	23	*P. strombulifera*; *P. reptans*; *P. abbreviata*; *P. torquata*; *P. sericantha*; *P. kuntzei*; *P. ruscifolia*; *P. fiebrigii*; *P. vinalillo*; *P. hassleri*; *P. humilis*; *P. rojasiana*; *P. rubriflora*; *P. campestris*; *P. affinis*; *P. elata*; *P. chilensis*; *P. nigra*; *P. caldenia*; *P. flexuosa*; *P. alpataco*; *P. alba*; *P. pugionata.*
PATAGONIAN AND CUYO REGION	5	*P. argentina*; *P. denudans*; *P. ruizlealii*; *P. castellanosii*; *P. calingastana.*

THE NATIVE AND INTRODUCED SPECIES OF PROSOPIS A GEOGRAPHICAL ENUMERATION

Numbers in parentheses represent the number of the species in the text.

ASIA AND NORTH AFRICA

NATIVE SPECIES

P. cineraria (1): Arabia; Iran, Afghanistan, Pakistan, and India.

P. farcta vars. **farcta** and **glabra** (2): Algeria and Tunisia; Egypt; Turkey and Cyprus; Syria and Israel; Iraq, Iran, Afghanistan, and Pakistan; USSR: Transcaucasia and Turkestan.

P. koelziana (3): Iran.

INTRODUCED SPECIES

P. pallida (29): India.

P. juliflora (35): Iraq, Pakistan, India, and Vietnam.

P. glandulosa (40): Southern Arabia, Pakistan, India, and Burma.

NOTES. Species successfully grown in the botanical garden at El Staff in middle Egypt: **P. alba, P. nigra, P. laevigata** (? sub **P. chilensis** and **P. dulcis**), **P. glandulosa, P. affinis** (sub **P. nandubay**), **P. kuntzei** (sub **P. kunzii**), **P. pubescens, P. strombulifera,** and the Oriental **P. cineraria** (sub **P. spicigera**); see Warda H. Bircher, *Gardens of the Hesperides*, 343–347. 1960.

TROPICAL AFRICA: one native species.

P. africana (4): Senegal, Guinea-Bissau to Nigeria, Cameroons, Sudan, Uganda, and Ethiopia.

SPECIES IN CULTIVATION
P. juliflora var. **juliflora** (35): Senegal.

SOUTH AND SOUTHWEST AFRICA: introduced species only.

P. pubescens (9).
P. chilensis var. **catamarcana** (34).
P. glandulosa (40).

PACIFIC ISLANDS (Hawaii, Marquesas, and the Philippines): introduced species only.

P. pallida formae **pallida** and **armata** (29).
P. juliflora (35).

AUSTRALIA: introduced species only.

P. pallida (29): only in cultivation.
P. chilensis? (34).
P. juliflora (35): Queensland.
P. glandulosa (40).
P. velutina (43): cultivated.

AMERICA: native species only.

UNITED STATES (continental): 5–7 species; none endemic.

P. strombulifera? (5): California.
P. reptans var. **cinerascens** (6): Texas, Oklahoma, and southeastern Colorado.
P. pubescens (9): Texas to southern California and southern Utah.
P. articulata (31): Arizona.
P. laevigata (38): Texas, rare.
P. glandulosa vars. **glandulosa, prostrata,** and **torreyana** (40): California to Kansas, Texas, and Louisiana.
P. velutina (43): Southern Arizona, California.

MEXICO: 9 native species; 3 endemic.

P. reptans var. **cinerascens** (6).
P. pubescens (9).
P. palmeri (10).
P. articulata (31).

P. tamaulipana (33).
P. juliflora (35).
P. laevigata (38).
P. glandulosa vars. **glandulosa, torreyana,** and **prostrata** (40).
P. velutina (43).

CENTRAL AMERICA (Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama).

P. juliflora (35).

ANTILLES (West Indian Islands: Cuba, Hispaniola, Jamaica, Puerto Rico, and many smaller islands): probably only species introduced from the mainland.

P. pallida (29): **including P. limensis.**
P. juliflora (35).
P. glandulosa (40): cultivated in Puerto Rico; see León & Alain, Fl. Cuba 2: 251. *fig. 108.* 1951.

VENEZUELA

P. juliflora (35).

COLOMBIA

P. pallida (29).
P. juliflora (35).

ECUADOR

P. pallida (29).
P. juliflora vars. **juliflora** and **inermis** (35).

PERU: 5–6 species, all native; none endemic.

P. strombulifera? (5).
P. reptans (6).
P. pallida (29): including **P. limensis.**
P. chilensis (34).
P. juliflora vars. **juliflora, horrida,** and **inermis** (35).
P. laevigata var. **andicola** (38).
P. alba var. **panta** (42).

BOLIVIA: 7–8 native species; none endemic.

P. ferox (12).
P. kuntzei (16).
P. ruscifolia (17).
? **P. affinis** (30).
P. chilensis (34).
P. nigra (36).
P. laevigata var. **andicola** (38).
P. alba var. **panta** (42).

CHILE: 6 native species; 2 endemic.

P. strombulifera (5).
P. burkartii (11).
P. tamarugo (13).
P. chilensis var. **chilensis** (34).
P. flexuosa (39): including **P. fruticosa.**
P. alba var. **panta** (42).

PARAGUAY: 11 native species; 2 endemic.

P. kuntzei (16).
P. ruscifolia (17).
P. fiebrigii (18).
P. vinalillo (19).
P. hassleri (20).
P. rojasiana (26).
P. rubriflora (27).
P. affinis (30).
P. elata (32).
P. nigra (36).
P. alba var. **panta** (42).

BRAZIL: 3 native species on very small areas, 1 introduced; none endemic.

P. ruscifolia (17): Piauhy/Parahyba (very local, introduced?).
P. rubriflora (27): extreme south of Mato Grosso.
P. affinis (30): extreme southwestern Rio Grande do Sul.
P. juliflora (35): *sensu stricto*, *haud sensu* Bentham in Fl. Brasil., 1876; introduced, cultivated, northern states.

URUGUAY: 3 native species.

P. affinis (30).
P. nigra (36).
P. alba (42).

ARGENTINA: native species only, ca. 28; 13 endemic. Center of polymorphism of the genus.

P. strombulifera vars. **strombulifera** and **ruiziana** (5).
P. reptans var. **reptans** (6).
P. abbreviata (7).
P. torquata (8).
P. ferox (12).
P. argentina (14).
P. sericantha (15).
P. kuntzei (16).
P. ruscifolia (17).
P. fiebrigii (18).
P. vinalillo vars. **vinalillo** and **parvifolia** (19).
P. hassleri vars. **hassleri** and **nigroides** (20).
P. denudans vars. **denudans, patagonica,** and **stenocarpa** (21).

P. ruizleali (22).
P. castellanosii (23).
P. calingastana (24).
P. humilis (25).
P. campestris (28).
P. affinis (30).
P. elata (32).
P. chilensis vars. **chilensis, riojana,** and **catamarcana** (34).
P. nigra vars. **nigra, ragonesei,** and **longispina** (36).
P. caldenia (37).
P. laevigata var. **andicola** (38).
P. flexuosa formae **flexuosa** and **subinermis** (39).
P. alpataco (41).
P. alba vars. **alba** and **panta** (42).
P. pugionata (44).

(To be concluded)

MAGNOLIACEAE HARDY IN TEMPERATE NORTH AMERICA [1]

STEPHEN A. SPONGBERG

MAGNOLIACEAE A. L. de Jussieu, Gen. Pl. 280. 1789, "Magnoliae," nom. cons.

(MAGNOLIA FAMILY)

Evergreen or deciduous trees or shrubs, the wood and bark often containing aromatic oils or mucilaginous substances; buds enclosed by stipular scales and the branchlets with conspicuous annular stipular scars at the nodes. Leaves conduplicate in bud, alternate, occasionally crowded into

[1] This treatment of the Magnoliaceae is the third published contribution in a series of treatments of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum of Harvard University and the purpose of which is to provide a modern, accurate account of the woody plants encountered in cultivation in the cooler temperate regions of North America. It is hoped that these treatments will eventually form the basis of a new manual of cultivated woody plants. The first paper in this series was published in the Journal of the Arnold Arboretum **56**: 1–19. 1975. Reference should be made to the introductory paragraphs of that paper for matters concerning area covered, taxa included, and the general philosophy of these treatments.

On the one-hundredth anniversary of his birth, it is with pleasure and admiration that this treatment of the Magnoliaceae is dedicated to the memory of ERNEST HENRY WILSON (1876–1930), indefatigable plant hunter and late Keeper of the Arnold Arboretum. It was through Wilson's efforts that many of the most ornamental taxa of *Magnolia* were introduced into cultivation in western gardens, and our knowledge of the genus and family has been greatly augmented by the specimens and information he collected on his several expeditions to eastern Asia.

Many individuals have made generous contributions of their time, advice, and knowledge during the preparation of this treatment, and I should like to thank Drs. R. A. Howard, L. M. Perry, K. R. Robertson, B. G. Schubert, P. F. Stevens, C. E. Wood, Jr., and R. E. Weaver, Jr., Miss K. Clagett, and Mrs. I. H. Burch, all of the Arboretum staff, for their freely given help. Particular thanks are also extended to Dr. N. G. Miller for his contribution of unpublished information, his collaboration on the treatment of *Liriodendron*, and his alcohol-preserved collections from which the illustrations for that genus were prepared; to Mr. B. H. Tiffney for data concerning the seeds and fossil distribution of *Magnolia*; and to the curators of the herbaria at Kew, the United States National Arboretum, and the National Science Museum, Tokyo, for the loan of herbarium specimens. Numerous friends and colleagues have also given freely of their time and advice and have supplied information, and to them I am greatly indebted. They include Dr. T. R. Dudley, Dr. J. M. Fogg, Jr., Miss J. deN. Henry, Mrs. J. W. Hill, Mr. H. G. Hillier, Mr. C. R. Lancaster, Dr. E. McClintock, Dr. J. C. McDaniel, Mr. B. Mulligan, Mr. N. Treseder, and Mr. J. C. Williams; I also thank my wife, Harmony, for help in many ways.

The illustrations are the careful work of Robin S. Lefberg and were prepared, when possible, from living or alcohol-preserved specimens collected in the Arnold Arboretum. Additional specimens collected at the Arboretum of the Barnes Foundation, the Henry Foundation for Botanical Research, and the Strybing Arboretum have been utilized, and thanks are due Dr. R. Simmers for providing material of *Magnolia macrophylla* collected in Tennessee.

Special thanks and gratitude are extended to an anonymous donor whose generous gift for this project has made and continues to make our work possible. In

false whorls, stipulate, the stipules free or adnate to and leaving scars on the adaxial surfaces of the petioles; leaf blades with pinnate venation, simple or lobed, the bases sometimes cordate to auriculate, the apices occasionally emarginate. Flowers solitary, terminal or axillary, perfect or rarely imperfect (*Kmeria*), in bud enclosed by one or more deciduous stipular bracts. Perianth of (5–)6–9–numerous, free, subsimilar or dimorphic tepals (in *Liriodendron* clearly differentiated into sepals and petals) in (2 or) 3 or sometimes more whorls, the tepals usually fleshy. Stamens numerous, spirally arranged on an elongate floral axis, 2-locular, the connectives often produced into short appendages, the anther sacs introrsely to extrorsely longitudinally dehiscent. Gynoecia comprised of numerous (rarely 1 or few) spirally arranged, free or basally concrescent, conduplicate carpels, the carpels usually closely imbricated on an elongate floral axis and contiguous with the androecium below (sessile) or separated from the androecium by a short gap on the floral axis (stipitate); carpels 2–6-ovulate, the ovules anatropous, bitegmic, crassinucellar. Fruits usually conelike aggregates of free or basally concrescent, dehiscent (or rarely indehiscent) follicles or conelike aggregates of deciduous samaras, rarely capsular. Seeds 1 or more per follicle or samara, the seed coat usually comprised of an outer, fleshy, aril-like layer and a hard, bony, inner layer, the small embryo embedded in copious oily endosperm. Base chromosome number = 19. (Tulipiferae Ventenat; including Liriodendraceae F. A. Barkley, excluding Illiciaceae Hu and Schisandraceae Blume.) TYPE GENUS: *Magnolia* L.

About twelve genera and 200 species in two tribes distributed in temperate and tropical eastern and southeastern Asia and in the Western Hemisphere in eastern North America from southern Canada southward through the West Indies and Central America to eastern Brazil; absent from Europe, Africa, Australasia, and Polynesia. Numerous species of several genera are of great importance as horticultural subjects, while other species are valued for their timber. Three genera are cultivated in our area, while species of *Manglietia* Blume (ca. 25 species of subtropical and tropical Asia) and *Talauma* Jussieu (ca. 40 species of subtropical and tropical Asia, southern Mexico, and the West Indies to Brazil) are occasionally cultivated south and west of our range in the United States. Because species of these two genera might be grown within our range in the collections of a few specialists, they are included in the key to the genera.

Owing to its position as one of the least derived and most ancient taxa of angiosperms, the Magnoliaceae has been the subject of considerable interest and numerous investigations, and a large body of literature concerning the biology of the family has accumulated. The references included in this paper are by no means all-inclusive but have been selected

addition, our deepest thanks are extended to the Director and trustees of the Stanley Smith Horticultural Trust for a grant that has made possible the preparation of illustrations to accompany these treatments. S. A. S.

to cover most aspects of the biology of the family and to include summary papers containing extensive bibliographies. In addition to the papers cited in the references, numerous articles of taxonomic importance or of limited specific content have been cited in the discussions of particular species. The discussions in Bean (1973) should be consulted for much historical and cultural information not included here.

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KEY TO THE GENERA OF MAGNOLIACEAE IN CULTIVATION

1. Fruits comprised of conelike aggregates of follicles, the follicles persistent on the floral axis; plants evergreen or deciduous, the leaves simple, not lobed, occasionally cordate to auriculate at base or emarginate at apex. Magnolieae. ..... 2.
   2. Flowers terminal; gynoecia sessile (or rarely short-stipitate in *Magnolia*); plants evergreen or deciduous. ..... 3.
      3. Mature follicles free, dehiscent along the abaxial sutures. ..... 4.
         4. Carpels with 2 ovules, the follicles with 2 seeds or sometimes 1 or none through abortion; plants evergreen or deciduous. ..... 1. *Magnolia.*
         4. Carpels with 4 or more ovules, the follicles with 4 or more seeds, sometimes fewer through abortion; plants evergreen. ..... *Manglietia.*
      3. Mature follicles free or basally concrescent, circumscissile, the upper portions falling away individually or in irregular clusters. ..... *Talauma.*
   2. Flowers axillary; gynoecia stipitate; plants evergreen. ..... 2. *Michelia.*
1. Fruits comprised of conelike aggregates of closely imbricated, 2-seeded samaras, the samaras falling at maturity, leaving a persistent spindle-shaped floral axis; plants deciduous, the leaves variously lobed. Liriodendreae. ..... 3. *Liriodendron.*

Tribe MAGNOLIEAE

1. **Magnolia** Linnaeus, Sp. Pl. 1: 535, 536. 1753; Gen. Pl. ed. 5. 240. 1754.

Evergreen, deciduous, or sometimes partially evergreen trees or shrubs of sympodial growth; bark often smooth, lenticellate, or sometimes rough and deeply furrowed, often silvery- or pewter-gray, the branchlets with continuous or septate pith; winter buds of two types, vegetative and mixed, enclosed by stipular scales, the mixed buds terminal and the stipular scales enclosing a terminal flower primordium subtended by one or more internodes with axillary vegetative buds at the nodes. Leaves alternate, sometimes crowded into false whorls, petiolate, stipulate, the stipules caducous, either free from the petioles or adnate to and leaving scars on the adaxial surfaces of the petioles; leaf blades thickly coriaceous to membranaceous, entire, sometimes cordate to auriculate at base or emarginate at the apex. Flowers usually fragrant, often large and showy, protogynous, beetle-pollinated, terminal, solitary, appearing before the leaves in spring (precocious) or with the leaves; within the mixed buds the flowers enclosed by one or more deciduous stipular (spathaceous) bracts, each bract leaving an annular scar on the pedicel. Tepals (5–)6–9–numerous (up to ca. 33), white or pink to purple, occasionally greenish or clear yellow, in whorls of 3, occasionally more, subsimilar or sometimes the outer whorl reduced in size and calyxlike. Stamens numerous, deciduous after anthesis, poorly differentiated into filaments and connectives, the connectives often produced into an appendage at the apex, the anther sacs introrsely or laterally dehiscent. Gynoecia sessile or rarely short-stipitate, cylindric to subglobose, the carpels with 2 ovules, the styles recurved, with stigmatic papillae along their adaxial surfaces. Fruits subglobose to cylindric conelike aggregates of follicles, the aggregates often asymmetrical from follicle (seed) abortion, at maturity the follicles free from one another and longitudinally dehiscent along their abaxial sutures. Seeds 1 or 2, suspended on thin threads (the elongated vessel elements of the funiculi and placentae), the seed coats with an aril-like, orange, red, or pink outer layer and a hard, bony inner layer. (*Buergeria* Sieb. & Zucc.; *Lassonia* Buc'hoz; *Tulipastrum* Spach; *Yulania* Spach.) TYPE SPECIES: *M. virginiana* L. (Name commemorating Pierre Magnol, 1638–1715, professor of botany and medicine and one-time director of the botanical garden at Montpellier, France.) — MAGNOLIA.

Approximately 80 species in two subgenera and 11 sections distributed in regions of temperate to tropical climates of eastern Asia from Manchuria, Korea, and Japan southward through China and the eastern Himalayan region to Java in the Malay Archipelago, and in the Western Hemisphere from southern Canada southward through the eastern United States, the West Indies, Mexico, and Central America to southeastern Venezuela. Several species of temperate areas in Asia have not yet been introduced into western horticulture. All of those that have, as well as those

North American species that are hardy within our area, are highly desirable ornamentals, and the genus is one of the most important groups of ornamental woody plants.

In nature, each species of *Magnolia* appears to occupy an exclusive range or habitat, thus precluding natural hybridization between species, but in cultivation several interspecific hybrids, some of considerable ornamental value, have occurred spontaneously or have been produced intentionally. Moreover, the ease with which species hybridize has stimulated ambitious breeding programs undertaken by several horticulturists. Within subgenera there are few barriers to hybridization between taxa of the same or different sections; however, substantial barriers between subgenera undoubtedly exist, inasmuch as no hybrids between species of the two subgenera have been recorded.

Most species of *Magnolia* are variable, and a great number of individual plants of horticultural value have been designated as cultivars. Moreover, several of the important hybrids have not been given specific epithets but are known chiefly by cultivar names. Therefore, outstanding cultivars have been briefly described or mentioned below, particularly when they are widespread in gardens or represent a particular species or hybrid group in cultivation. No attempt has been made, however, to account for all the cultivars of a particular species or hybrid group. Persons interested in *Magnolia* cultivars are encouraged to consult the checklist of Fogg and McDaniel (1975), in which a nearly complete and current listing of all cultivars of *Magnolia* has been assembled.

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KEY TO THE SUBGENERA OF MAGNOLIA

1. Anthers dehiscing introrsely; flowers neither appearing before the leaves nor with an outer whorl of sepaloid tepals; plants evergreen or deciduous. ..... Subg. MAGNOLIA.
1. Anthers dehiscing laterally or sublaterally; flowers precocious, appearing before the leaves and/or with a much reduced outer whorl of sepaloid tepals; plants deciduous. ..... Subg. YULANIA (see p. 280).

MAGNOLIA subg. MAGNOLIA

Evergreen or deciduous trees and shrubs, the flowers appearing with the leaves; tepals subsimilar, the outer whorl like the inner whorls, never reduced in size and sepaloid; anther sacs introrsely dehiscent.

Eight sections, two of American distribution in both hemispheres, five of Asiatic distribution, and one with species in North America and eastern Asia; species of six of these sections represented in cultivation in our area.

KEY TO THE SPECIES AND SELECTED HYBRIDS OF MAGNOLIA SUBG. MAGNOLIA IN CULTIVATION

1. Stipules free, not adnate to and not leaving scars on the adaxial surfaces of the petioles; plants evergreen. ..... 2.
   2. Gynoecia sessile, the floral axis with stamens or stamen scars contiguous with the lowermost carpels or follicles. ..... 3.
      3. Tepals 7.5–12 cm. long; stamens 13–21 mm. long, yellowish; fruit aggregates ovoid, 5.5–7.5 cm. long. ..... 1. *M. grandiflora*.
      3. Tepals 5.5–9 cm. long; stamens ca. 12 mm. long, rosy-purple; fruit aggregates ca. 4 cm. long, rarely developed. ..... 23. *M. virginiana* × *M. grandiflora*.
   2. Gynoecia stipitate, the floral axis with stamens or stamen scars not contiguous with the lowermost carpels or follicles. ..... 2. *M. nitida*.
1. Stipules adnate to the petioles, leaving scars on the adaxial surfaces of the petioles; plants evergreen or deciduous. ..... 4.
   4. Plants evergreen. ..... 5.
      5. Stipule scars large, extending almost the entire length of the petiole to the base of the leaf blade. ..... 6.
         6. Petioles (2.6–)3.5–6.7(–8.7) cm. long; leaf blades thickly coriaceous, the lower surfaces pale green or yellowish; fruit aggregates 6.7–9.5 cm. long. ..... 3. *M. delavayi*.
         6. Petioles 1.5–2(–3) cm. long; leaf blades thinly coriaceous to membranaceous, the lower surfaces glaucous, rarely green; fruit aggregates 2–5 cm. long. ..... 4. *M. virginiana*.

5. Stipule scars very small, at the base of the petioles, often obscure. . . . . 23. *M. virginiana* × *M. grandiflora*.

4. Plants deciduous. . . . . 7.

7. Leaves crowded into false whorls at the ends of branchlets, distinctly alternate on new shoots; leaf blades large or very large, (10–)18–60(–100?) cm. long. . . . . 8.

8. Leaf blades cordate to auriculate at base. . . . . 9.

9. Lower surfaces of the leaf blades, stipules, carpels, and follicles pubescent. . . . . 10.

10. Trees; stamens 15–18 mm. long; fruit aggregates subglobose to globose. . . . . 5. *M. macrophylla* subsp. *macrophylla*.

10. Large shrubs; stamens 11–13 mm. long; fruit aggregates subcylindric to ovoid. 5. *M. macrophylla* subsp. *ashei*.

9. Lower surfaces of the leaf blades, stipules, carpels, and follicles glabrous. . . . . 11.

11. Stamens 8–15 mm. long; gynoecia ca. 2.5 cm. long at anthesis; fruit aggregates 6.5–11 cm. long. . . . . 6. *M. fraseri* var. *fraseri*.

11. Stamens 4–6 mm. long; gynoecia ca. 1.5 cm. long at anthesis; fruit aggregates 3.5–5.5(–6) cm. long. . . . . 6. *M. fraseri* var. *pyramidata*.

8. Leaf blades cuneate to rounded at base. . . . . 12.

12. Hairs on the lower surfaces of the leaf blades usually with rust-colored pigment; tepals broadly obovate, 5.5–6 cm. long; stamens rosy-crimson throughout. . . . . 24. *M.* × *wieseneri*.

12. Hairs on the lower surfaces of the leaf blades lacking rust-colored pigment; tepals obovate to oblong-elliptic or spatulate, 8–12 cm. long; stamen filaments tinged reddish, the anther sacs creamy white or yellowish. . . . . 13.

13. Flowers with an offensive odor; fruit aggregates 7–10 cm. long; small trees of open habit. . . 7. *M. tripetala*.

13. Flowers pleasantly fragrant; fruit aggregates (9–)13.5–20 cm. long; large, widely branching trees. . . . . 14.

14. Leaf blades mostly oblong-obovate, with acute to rounded apices; young branchlets purplish or silvery; fruit aggregates with the lowermost follicles concave, decurrent along the floral axis. . . . . 8. *M. hypoleuca*.

14. Leaf blades mostly elliptic-obovate, sometimes deeply emarginate at apex; young branchlets yellowish or yellowish-gray; fruit aggregates with the lowermost follicles convex, not decurrent along the floral axis. . . . . 9. *M. officinalis*.

7. Leaves distinctly alternate, not crowded into false whorls at the ends of branchlets; leaf blades of moderate size, not exceeding 23 cm. in length. . . . . 15.

15. Flowers and fruit aggregates held ± erect on the branchlets. . 16.

16. Anthers yellowish, the connectives with short, acute appendages. . . . . 17.

17. Pith septate; tepals 6–15, 3–5(–9) cm. long; leaf blades (3.5–)6.5–10.5(–17.7) cm. long, generally narrowly oblong to elliptic or ovate. ..... 4. *M. virginiana.*
17. Pith incompletely septate; tepals 9, 7–9 cm. long; leaf blades (5.5–)12–17.5(–22) cm. long, broadly elliptic to oblanceolate. ..... 25. *M.* × *thompsoniana.*

16. Anthers rosy-crimson, rounded or blunt at the apices, the connectives only rarely produced into apiculate appendages. ..... 24. *M.* × *wieseneri.*

15. Flowers and fruit aggregates held nodding or pendent on the branchlets. ..... 18.

18. Branchlets becoming dark reddish- or purplish-brown. .. 19.

19. Leaf blades elliptic, broadly ovate, or usually obovate, (4.5–)7–9(–14.5) cm. wide, generally rufous-pubescent on the under surfaces; stamens 12–17 mm. long. .... 10. *M. globosa.*

19. Leaf blades elliptic or usually lanceolate to oblong-ovate, (2.5–)3–7(–11) cm. wide, generally yellowish- or silvery-pubescent on the under surfaces; stamens 9–12 mm. long. ..... 11. *M. wilsonii.*

18. Branchlets becoming light brown or silvery-tan. ..... 20.

20. Some or all hairs on the lower surfaces of the leaf blades with rust-colored pigment, the hairs ± straight; leaf blades usually broadly obovate. .... 12. *M. sieboldii* subsp. *sieboldii.*

20. Hairs on the lower surfaces of the leaf blades clear, lacking rust-colored pigment, the hairs ± crinkled; leaf blades usually broadly elliptic to obovate. .... 12. *M. sieboldii* subsp. *sinensis.*

MAGNOLIA sect. THEORHODON Spach, Hist. Nat. Veg. Phanerog. 7: 470. 1839.

Evergreen trees, variously pubescent; stipules free from the petioles; gynoecia sessile, the stamens and carpels contiguous on the floral axis. TYPE SPECIES: *M. grandiflora* L.

About fifteen species of the Americas; with the exception of *Magnolia grandiflora*, all of tropical distribution. Several species of sect. THEORHODON of tropical areas have been introduced into cultivation but are not known to be hardy within our region.

1. **M. grandiflora** Linnaeus, Syst. Nat. ed. 10. 2: 1082. 1759.

FIGURE 1.

Large, evergreen trees, often of pyramidal habit, sometimes attaining 25 or 30 m., the bark brown or gray, with thin, tightly appressed platelets; branchlets stout, with septate pith, at first densely felted with rufous, yellowish, or silvery hairs, the older growth eventually glabrous, becoming dark blackish-brown; buds densely sericeous with rufous to ± silvery

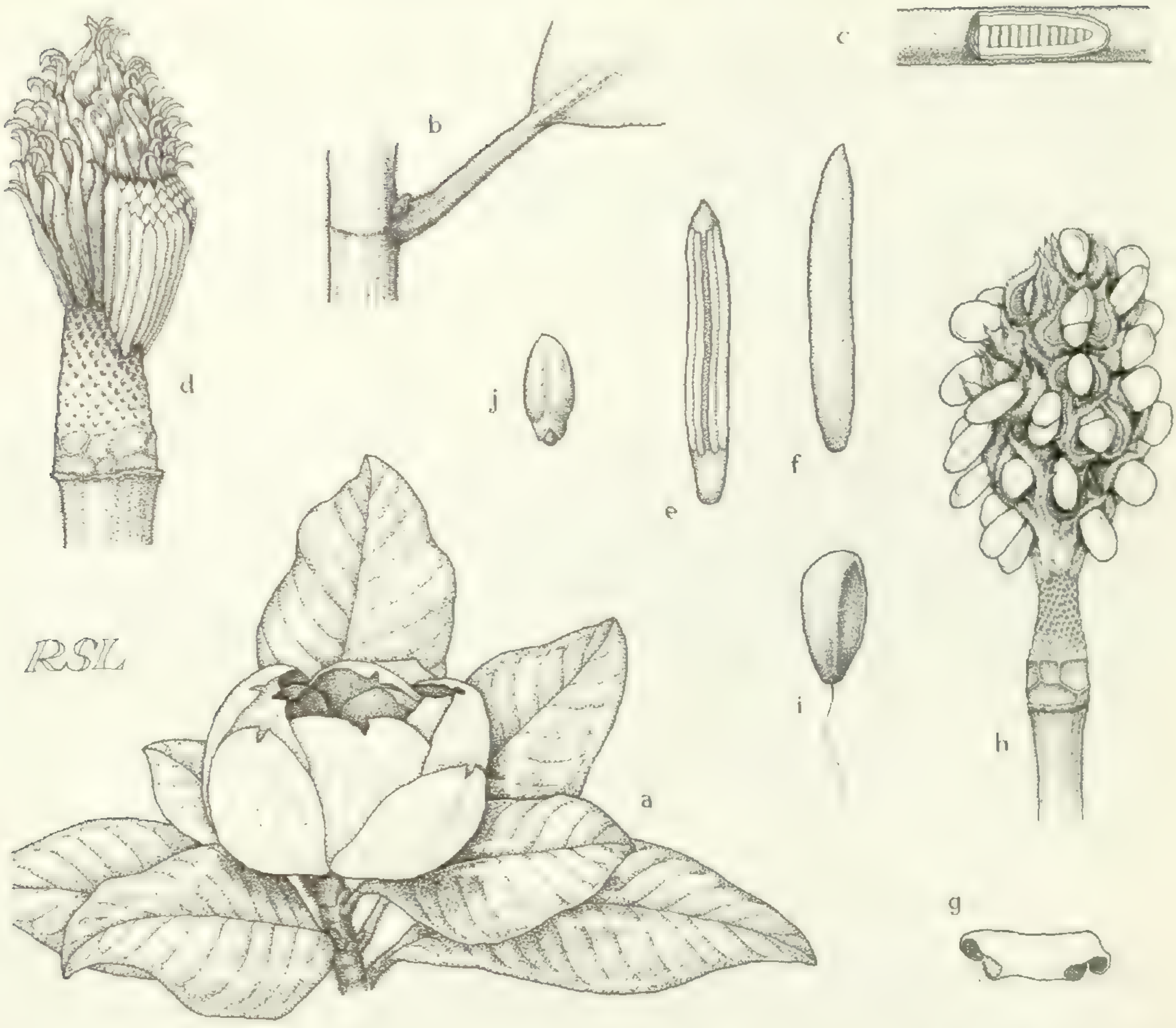


FIGURE 1. **Magnolia** sect. **Theorhodon.** a–j, *M. grandiflora*: a, habit of flowering branchlet of 'Praecox Fastigiata', × ⅓; b, branchlet and petiole, showing lack of stipule scar on petiole, × ¾; c, section of branchlet showing septate pith, × 1; d, flower with tepals removed, showing androecium (many stamens removed) and gynoecium, × 1; e, adaxial surface of stamen, showing introrse lines of dehiscence of pollen sacs, × 2; f, abaxial surface of stamen, × 2; g, transverse section through stamen, × 6; h, fruit aggregate, × ½; i, seed with outer seed coat intact, × 1; j, seed with outer seed coat removed, × 1.

hairs. Leaves falling in spring at 2 years of age; petioles stout, 9–27 mm. long, densely felted with rufous or yellowish hairs, sometimes becoming subglabrous, the stipules free and the petioles lacking stipule scars on the adaxial surfaces; leaf blades stiffly coriaceous, variable in size and shape, (5–)7.9–20(–25.5) cm. long, (2.9–)6–8.7(–14.4) cm. wide, narrowly to broadly elliptic, lanceolate, oblanceolate, ovate, or usually broadly ovate to ± subglobose, with attenuate, acute, cuneate, or subrounded, often oblique bases, undulate margins, and obtuse to short-acuminate, rarely retuse apices; upper surfaces of the blades dark green (or rarely variegated), brilliantly glossy, glabrous, when dried finely reticulated in a ± honeycomb pattern; lower surfaces thickly to thinly felted with rufous hairs or occasionally subglabrous with hairs only along the elevated midveins. Flowers large, heavily fragrant, held erect on stout, felted to sericeous pedicels; tepals 9 or 12 (or rarely to 25), thick and fleshy, creamy white, broadly spatulate to broadly obovate or ± orbicular,

7.5–12 cm. long, 4–9 cm. wide; stamens numerous, 13–21 mm. long, with purplish filaments; gynoecia 2–2.5 cm. long at anthesis, the carpels densely sericeous with silvery hairs, the styles glabrous. Fruit aggregates ovoid, 5.5–7.5 cm. long, yellowish- or silvery-tan, the follicles finely sericeous, with short, ± ascending stylar beaks; lowermost follicles basally decurrent along the floral axis; seeds ca. 12 mm. long, the outer seed coats red, the inner ones ivory. $2n = 114$. (*M. foetida* Sarg.) — BULL BAY.

Native to the Coastal Plain of the southeastern United States from North Carolina south to central Florida and west to eastern Texas and Arkansas (see E. L. Little, Jr., Atlas of U. S. Trees **1**: *map 141-E.* 1971); widely cultivated throughout the world.

Among the very numerous cultivars of *Magnolia grandiflora*, some are deserving of mention here, while others have been described by McDaniel (Newsl. Am. Magnolia Soc. 9(3): 3–7. 1973). For a complete listing of named cultivars, reference should be made to the checklist of Fogg and McDaniel (1975), in which more than 150 cultivars of *M. grandiflora* are accounted for. It should be noted that 'Galissoniensis' (= *M. grandiflora* f. *galissoniensis* K. Koch, Dendr. 1: 368. 1869; see also, N. Treseder, Newsl. Am. Magnolia Soc. 6(1): 3. 1969), a very hardy clone listed by Rehder in his *Manual* (1940), is apparently not in cultivation in the United States (*fide* Fogg & McDaniel, 1975). 'Exmouth' (= *M. grandiflora* f. *lanceolata* (Aiton) Rehder, Bibl. Cult. Trees Shrubs 180. 1949; γ *lanceolata* Aiton, Hort. Kew. 2: 251. 1789; var. *exoniensis* Hort. ex Loudon, Arb. Brit. 1: 261. 1838; cv. Exoniensis; see also Bot. Mag. *t. 1952*. 1817) is an old clone of narrow pyramidal habit with oblong-elliptic to oblong-lanceolate leaves finely pubescent on the lower surfaces. 'St. Mary' (see H. H. Hume, Morris Arb. Bull. 12: 16. 1961) is a conical tree with leaves densely dark brown pubescent beneath and with cup-shaped flowers that are produced freely even when the plant is young. 'Goliath' (see J. G. Millais, 1927, p. 140, and Gard. Chron. III. **148**: 309. 1960) is noteworthy for its short, subglobose leaves with blunt apices and glabrous or thinly pubescent under surfaces and for its large flowers that are produced until late in the growing season. 'Praecox Fastigiata' is also noted for its continual flowering until late into the growing season, as well as for its fastigiate habit. Finally, 'Charles Dickens' (see J. W. Templeton, Morris Arb. Bull. **16**: 8, 9. 1965), $2n = 76$, a tetraploid, is noted for its large, ovoid, bright red fruit aggregates and oblong seeds. Its chromosome number suggests that it comprises a hybrid between *M. grandiflora*, $2n = 114$, and some other species (see J. C. McDaniel, Newsl. Am. Magnolia Soc. 7(2): 4–7, 1970). The documented hybrids between *M. virginiana* and *M. grandiflora*, often referred to as the Freeman hybrids, are described below.

MAGNOLIA sect. GYNOPODIUM J. E. Dandy, Bot. Mag. **165**: *in nota sub t. 16.* 1948.

Glabrous evergreen trees and shrubs; stipules free from the petioles; gynoecia short-stipitate, the stamens and carpels not contiguous on the floral axis. TYPE SPECIES: *M. nitida* W. W. Smith.

Four species of eastern Asia. Only the type species is known in cultivation.

2. **M. nitida** W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **12**: 212. 1920.

Glabrous evergreen trees or large shrubs, in age to ca. 15 m., with rough, ashy-brown bark; branchlets yellowish-green, becoming dark brown, with conspicuous encircling stipule scars at the nodes, the internodes short, ± regularly spaced; pith septate. Leaves persistent or occasionally falling under severe winter conditions; petioles 1.5–2.5 cm. long, yellowish-green, the stipules free and the petioles without scars on the adaxial surfaces; leaf blades stiffly coriaceous, (5–)8–11.5(–12.7) cm. long, (2–)3–5.5(–8.2) cm. wide, elliptic, oblong-lanceolate or oblong-oblanceolate, with acute or short-acuminate, rarely emarginate apices, entire margins, and cuneate, obtuse, or rounded bases; upper surfaces of the leaf blades dark glossy green, the venation indistinct; lower surfaces pale green, not shining. Flowers fragrant, becoming ± saucer-shaped, borne erect at the ends of branchlets on stout pedicels 3–12 mm. long; tepals 9–12, creamy white, the outer 3 flushed purplish on the abaxial surfaces, fleshy, ca. 4–5 cm. long, spatulate to obovate; stamens numerous, 10–17 mm. long; gynoecia short-stipitate, green, the stigmas red. Fruit aggregates bright green, ± cylindric, 3–7 cm. long; seeds with bright orange outer seed coats. $2n = 38$.

Native to northwestern Yunnan Province, China, northeastern Upper Burma, and southeastern Tibet; marginally hardy within the southern part of our area.

Inasmuch as I have not seen an adequate number of specimens on which to base this description, some of the information included above, particularly concerning the flowers, has been based on J. E. Dandy's article (Bot. Mag. **165**: *t. 16.* 1948) and Johnstone's description (1955, pp. 141–143, *pl. 14* & *fig. 20*). It is noted in *Hilliers' Manual* (1973, p. 182) that the new shoots of *Magnolia nitida* "have an almost metallic lustre."

MAGNOLIA sect. GWILLIMIA De Candolle, Reg. Veg. Syst. Nat. 1: 455, 548. 1817, emend. J. E. Dandy, Camellias and Magnolias, Roy. Hort. Soc. Conf. Rep. 67. 1950.

Evergreen trees and shrubs; stipules adnate to the petioles, leaving

scars on the adaxial surfaces of the petioles; fruit aggregates comprised of follicles with short stylar beaks. TYPE SPECIES: *M. coco* (Lour.) DC.

Eleven to fourteen species of southeastern Asia. *Magnolia delavayi*, the only temperate species of the section, is marginally hardy in the southern part of our area. *Magnolia coco* (see Bot. Mag. **25**: *t. 977*. 1806), although not included here, is known to be cultivated in warmer temperate and subtropical areas of the United States.

3. **M. delavayi** Franchet, Pl. Delavayanae 33. *t. 9, 10*. 1889.

Large evergreen shrubs or trees to ca. 10 m., with dark brown, longitudinally fissured bark; branchlets stout, lenticellate, with continuous pith, greenish-tan, at first densely felted with appressed, yellowish-tan hairs, the older growth finely appressed-sericeous, particularly at the nodes, eventually glabrous. Leaves long-petiolate, the petioles (2.6–)3.5–6.7(–8.7) cm. long, often tuberculate, at first densely appressed-sericeous, in age ± glabrescent, the elongate stipule scars extending almost to the base of the blades; leaf blades thickly coriaceous, elliptic to ovate or oblong-ovate, rarely suborbicular, (10.4–)13–20(–30, *fide* Johnstone) cm. long, (4.3–)5–10.5(–16, *fide* Johnstone) cm. wide, with acute to rounded bases, undulate margins, and rounded to obtuse or occasionally retuse apices (the apex itself often very short-apiculate); upper surfaces of the blades dark, dull green, at first finely pubescent, soon glabrous, reticulate; lower surfaces at first finely pubescent over the entire surface, eventually glabrous, pale green or yellowish, the midveins and major lateral veins conspicuously elevated. Flowers fragrant, ± cup-shaped, borne on stout, glabrous or sericeous pedicels; tepals 9, fleshy, the outer 3 greenish-white, becoming reflexed, the inner 6 creamy white, spatulate to obovate, (5.5–)7–10 cm. long, 2.5–3.5 cm. wide, the inner tepals more slender; stamens numerous, 1.5–2 cm. long; gynoecia ovoid with ± acute apices, 3–4 cm. long at anthesis, usually finely pubescent with yellowish hairs, particularly at the base. Fruit aggregates 6.7–9.5 cm. long, ovoid-oblong, becoming light brown, usually with ± acute apices; follicles finely pubescent or subglabrous, with short, ± spreading stylar beaks. $2n = 38$.

Endemic to Yunnan and Szechwan provinces, China; rarely cultivated in the southern portion of our area.

The only other species cultivated in our region with which *Magnolia delavayi* might be confused is *M. grandiflora*. The two species can be distinguished easily, however, by a comparison of the petioles; long stipule scars occur on the petioles of *M. delavayi*, while scars are lacking on petioles of *M. grandiflora*. Moreover, the septate pith of branchlets of *M. grandiflora* also distinguishes that species from *M. delavayi*, which has continuous pith.

MAGNOLIA sect. MAGNOLIA.

Evergreen to deciduous trees or shrubs; stipules adnate to the petioles, the petioles with stipule scars on the adaxial surfaces; leaf blades glaucous beneath; anthers with the connectives produced into short, acute appendages. TYPE SPECIES: *M. virginiana* L.

A monotypic section comprised of only *Magnolia virginiana* of the eastern United States.

4. **M. virginiana** Linnaeus, Sp. Pl. 1: 535. 1753.

Deciduous, semievergreen or evergreen trees to 30 m., or often large, multiple-trunked shrubs of open, lax habit; bark on old limbs grayish-brown, with small platelets and irregularly furrowed; branchlets glabrous to densely sericeous with silvery hairs, green or yellowish-green, becoming purplish-brown; pith conspicuously septate; terminal winter (mixed) buds finely to thickly sericeous with silvery hairs. Leaves alternate, the yellowish-green petioles 1.5–2(–3) cm. long, subglabrous to finely sericeous, the elongate glabrous or pubescent stipule scars extending almost to the bases of the blades; leaf blades variable, narrowly oblong to elliptic, oblong-elliptic, ovate, or sublanceolate, rarely suborbicular, (3.5 -)6.5–10.5 (–17.7) cm. long, (1.5–)3.5–4.5(–6.5) cm. wide, tapering to rounded to acute or very rarely retuse apices and cuneate to acute bases, the margins entire, sometimes finely ciliate; upper surfaces of the blades lustrous green, rarely variegated, glabrous or often puberulent, particularly at base and along the light yellowish-green midveins; lower surfaces silvery-glaucous, rarely green, at first thickly sericeous with silvery hairs, becoming finely sericeous to puberulent. Flowers fragrant, creamy white, ± globose to cup-shaped, appearing with the leaves on stout, glabrous or sericeous pedicels; tepals 6–15, rarely more, the outer 3 becoming ± reflexed, the inner tepals 3–5(–9) cm. long, 1.2–2 cm. wide, spatulate to obovate or suborbicular, with rounded apices and short-clawed bases; stamens relatively few, ca. 9 mm. long, the anthers with short, acute appendages; gynoecia glabrous, greenish, ca. 1 cm. long at anthesis. Fruit aggregates becoming pinkish-red at dehiscence, finally dark purplish- or reddish-brown, ovoid, ellipsoid, or subglobose, (2–)3–4.5(–5) cm. long, the follicles with or without very short stylar beaks; seeds ca. 1 cm. long, the outer seed coats dark red. $2n = 38$. (*M. virginiana* var. *glauca* L.; *M. glauca* L.; including *M. virginiana* var. *australis* Sarg., *M. australis* Ashe.) — SWEET BAY.

Native to the Coastal Plain and adjacent Piedmont of eastern North America from Massachusetts and New York southward to Georgia and Florida and westward into eastern Texas, Arkansas, and Tennessee (see E. L. Little, Jr., Atlas of U. S. Trees 1: *map 142–E.* 1971).

Evergreen, semievergreen, or deciduous plants of *Magnolia virginiana* from the southern part of its range, usually developing a tree habit to 30 m., less often large multiple-trunked shrubs, with persistently sericeous branchlets, pedicels, and petioles, have been recognized as var. *australis* Sarg., Bot. Gaz. 67: 231. 1919 (*M. australis* Ashe), but this taxon is included here within the species. J. C. McDaniel, a noted student and authority on *Magnolia* who has made studies of the variation encountered in *M. virginiana*, is convinced that the recognition of var. *australis* (and perhaps yet another variety) is justified, and reference should be made to his major article on this subject (Morris Arb. Bull. 17: 7–12. 1966). However, while behavioral and other characters outlined by McDaniel are indeed evidence of differences between northern and southern populations of *M. virginiana*, it would seem that differences are to be expected within a wide-ranging species. Inasmuch as most of the characters are ill defined morphologically and are clinal over the range, a utilitarian taxonomy does not appear to result from the recognition of a southern variety.

Three hybrids involve *Magnolia virginiana* and species of sect. RYTIDOSPERMUM, namely *M. virginiana* × *M. hypoleuca*, *M. virginiana* × *M. macrophylla*, and *M. virginiana* × *M. tripetala*, the hybrid group that has received the collective name *M.* × *thompsoniana* (q.v.). The first two hybrids are not described here (but see under *M. hypoleuca* and *M. macrophylla*), inasmuch as I have not seen specimens documenting these hybrids and they are not known to me to be widely distributed in American gardens or arboreta.

A second group of hybrids involves *Magnolia virginiana* and species of sect. THEORHODON. The hybrid *M. virginiana* × *M. grandiflora* is described below, while *M. virginiana* × *M. guatemalensis*, although known to be hardy as far north as Maryland, is not accounted for here for the same reasons outlined above. It should also be noted that plants of *M. guatemalensis* J. D. Smith, Bot. Gaz. 47: 253. 1909, a species of sect. THEORHODON from Guatemala, have been distributed from the United States National Arboretum, but are not known by me to be hardy in our area.

MAGNOLIA sect. RYTIDOSPERMUM Spach, Hist. Nat. Veg. Phanerog. 7: 474. 1839.

Deciduous trees or large shrubs; leaves crowded into false whorls at the ends of branchlets, alternate and widely spaced on new shoots. TYPE SPECIES: *M. tripetala* L.

As defined here, three American species of the Temperate Zone (two comprised of two subspecies each) and three species of eastern Asia.

FIGURE 2. **Magnolia** sect. **Rytidospermum.** a–c, *M. hypoleuca*: a, flower, × ⅓; b, fruit aggregate with obsolete stylar beaks, × ½; c, seeds with the outer seed coats removed to show surface grooving of inner seed coats, × 1. d, habit of branchlet with fruit aggregate of *M. tripetala*, × ⅙. e–g, *M. macrophylla* subsp. *macrophylla*: e, fruit aggregate, × ½; f, seed with outer seed coat intact, × 1; g, seeds with outer seed coats removed, × 1. h, i, *M. macrophylla* subsp. *ashei*: h, lower portion of leaf showing auriculate base and stipules enclosing terminal bud, × ⅓; i, fruit aggregate, × ½.

5. **M. macrophylla** Michaux, Fl. Bor.-Am. 1: 327. 1803.

FIGURE 2, e–i.

Deciduous trees to 15 or rarely 20 m., usually of slender upright habit, occasionally widely branching, the bark on trunk and older limbs smooth,

light gray; branchlets stout, green, at first thickly tomentose with silvery hairs, becoming glabrous and reddish-brown, with prominent leaf scars clustered in groups (the internodes very short), the groups separated by elongated internodes; terminal winter (mixed) buds thickly tomentose with silvery hairs. Leaves crowded into false whorls at the ends of branchlets or alternate on new shoots; petioles stout, (3–)5.5–13(–15) cm. long, densely to finely tomentose like the young branchlets, sometimes glabrescent, with elongate stipule scars on the adaxial surfaces; leaf blades membranaceous, very large, (18–)24–60(–100?) cm. long, (8.9–)11–26(–32) cm. wide, broadly elliptic, oblanceolate, or oblong-oblanceolate with cordate to auriculate, rarely subtruncate bases, entire, often undulate margins, and rounded, obtuse, or acute apices; upper surfaces of the blades green, glabrous; lower surfaces of the blades chalky white to silvery-glaucous, sometimes glaucescent, finely pubescent over the entire surface, particularly on and along the conspicuously elevated midveins and major lateral veins, occasionally becoming subglabrous. Flowers fragrant, large, ± cup-shaped, held erect on stout, silvery-tomentose pedicels ca. 5 cm. long, subtended by a false whorl of leaves; tepals 9, irregular and unequal, the outer 3 greenish, usually narrowly spatulate, becoming yellowish and reflexed, the inner 6 creamy white, often purplish-spotted near the base on the adaxial surface, 14.5–20.5 cm. long, 5–14 cm. wide, broadly spatulate, elliptic, ovate, or suborbicular, with broad or abruptly constricted, short-clawed bases; stamens creamy white, very numerous, 15–18 mm. long; gynoecia 2–3 cm. long at anthesis, the carpels with densely silvery-pubescent ovaries and glabrous styles. Fruit aggregates subglobose to globose, 5.5–8 cm. long, rosy-colored at dehiscence, becoming grayish-brown; follicles pubescent, with stout beaks, or sometimes the beaks obsolete, the lowermost follicles dehiscing ± downward, with the floral axis forming an angle of ca. 90°; seeds 1–1.4 cm. long, the outer seed coats pinkish-red or coral red. $2n = 38$.

Native to rich woodlands of the southeastern United States in Georgia and Alabama to Louisiana northward to West Virginia, Kentucky, and Arkansas.

Plants developing a shrublike habit to 10 m., with the stout branchlets at first heavily glaucous and finely tomentose with silvery hairs, often with slightly smaller flowers (the largest tepals 10–13 cm. long, 3–6.5 cm. wide), the stamens 11–13 cm. long, and with the mature fruit aggregates subcylindric to ovoid, (4.5–)5–7 cm. long, the lowermost follicles and the floral axis forming an oblique angle, are recognized here as **Magnolia macrophylla** subsp. **ashei** (Weatherby) Spongberg, comb. et stat. nov. (BASIONYM: *Magnolia ashei* Weatherby, Rhodora **28**: 35. 1926). *Magnolia macrophylla* subsp. *ashei*, $2n = 38$, is apparently endemic to the panhandle of northwestern Florida, where it is most frequently encountered in the Knox Hill region of Walton County. While it has also been reported from eastern Texas (Vines, 1960), the records

are probably based on cultivated plants of *M. macrophylla* subsp. *macrophylla*.

The nature of the differences between plants of the two subspecies of *Magnolia macrophylla* (in habit, length of stamens, young branchlet characters, and shape of fruit aggregates), as well as their distinct geographical distribution in nature, suggests that the taxonomic treatment accorded these taxa as subspecies best reflects these differences while also recognizing their extremely close relationships.

A hybrid between *Magnolia macrophylla* subsp. *macrophylla* and *M. virginiana* has been produced, but since specimens of this hybrid have not been examined, it is not described here.

6. M. fraseri Walter, Fl. Carol. 159. 1788.

Small trees to ca. 14 m., usually of open, spreading habit, with smooth, brownish or grayish bark; branchlets slender to ± stout, glabrous, dark purplish- or reddish-brown, with prominent transverse-elliptic leaf scars clustered in groups (the internodes very short), the groups separated by elongated internodes; terminal winter (mixed) buds glabrous, purplish or greenish. Leaves crowded into false whorls at the ends of branchlets or alternate on new shoots; petioles slender, 3–6(–13) cm. long, glabrous, with elongate stipule scars on the adaxial surfaces; leaf blades membranaceous, broadly spatulate, elliptic, or broadly lanceolate, (11.3–)14.8–26.5(–53) cm. long, (5.5–)8.4–18(–29) cm. wide, with obtuse to acute apices, entire margins, and subcordate, rarely truncate, or usually auriculate bases; upper surfaces of the blades green, glabrous; lower surfaces glaucescent, the midveins and major lateral veins prominently elevated. Flowers sweetly scented, ± vase-shaped, becoming saucer-shaped, held erect on stout pedicels 2–3.5(–4) cm. long at the ends of branchlets, subtended by a false whorl of leaves; tepals 9, yellowish or creamy white, the outer 3 subequal or rarely longer than the inner 6, with broad bases, the inner 6 broadly spatulate, lanceolate, or obovate, with rounded to acute apices and narrow, ± clawed bases, (7–)8–12(–14) cm. long, 2.4–4.7 cm. wide; stamens numerous, 8–15 mm. long; gynoecia 2–2.8 cm. long at anthesis, glabrous. Fruit aggregates 6.5–11 cm. long, ellipsoid, bright red at dehiscence, becoming dark, purplish-brown, the follicles with long, spreading, hooked stylar beaks; seeds ca. 1 cm. long, the outer seed coats red. $2n = 38$. (*M. auriculata* Bartram.)

Native to rich forests in the mountains of the southeastern United States from Virginia and West Virginia south to Alabama and Georgia and west to Louisiana and eastern Texas (Jasper County).

Plants of the lower Piedmont and Coastal Plain of the southeastern United States from South Carolina into northern Florida and westward through Alabama and Mississippi to eastern Texas (Jasper and Newton counties) comprise *Magnolia fraseri* var. *pyramidata* (Bartram) Pampanini, Bull. Soc. Tosc. Ortic. 40: 230. 1915 (*M. pyramidata* Bartram,

M. auriculata β *pyramidata* Nuttall). Usually small trees (rarely to ca. 16 m.) of pyramidal form with ascending branches and leaves often ± pandurate or rhombic in outline, plants of var. *pyramidata*, $2n = 38$, can be distinguished from var. *fraseri* by their shorter stamens 4–6 mm. long, their smaller gynoecia ca. 1.5 cm. long at anthesis, and their shorter fruit aggregates 3.5–5.5(–6) cm. long. Miller (1975) states that "there is a gradual transition between [var.] *pyramidata* of Florida and [var.] *fraseri* of the mountains, since the Alabama and Georgia plants form a continuous sequence from north to south in these states." While Clark (1971) has totally submerged var. *pyramidata* within *M. fraseri*, the Piedmont and Coastal Plain plants are recognized here as a variety, since the two taxa, based on the wild and cultivated specimens examined during this study, can be distinguished by the characters outlined above.

Hybrids between *Magnolia fraseri* and *M. hypoleuca* and *M. fraseri* and *M. tripetala* have been produced by P. J. Savage, Jr., but are not described here because of their limited distribution in cultivation. (See discussion under *M. hypoleuca*.)

7. **M. tripetala** Linnaeus, Syst. Nat. ed. 10. 2: 1082. 1759.

FIGURE 2, d.

Small deciduous trees of open habit to 12 m., sometimes shrublike, with several limbs from near the base; bark smooth, ash-gray, lenticellate, with fine longitudinal fissures developing on old trunks; branchlets stout, brittle, brownish- or purplish-gray, with continuous pith and prominent transverse-elliptic or suborbicular leaf scars clustered in groups (the internodes very short), the groups separated by elongated internodes; terminal winter (mixed) buds large, purplish, glaucous. Leaves crowded into false whorls at the ends of branchlets or alternate on new shoots; petioles stout, (1–)2–3.5 cm. long, yellowish-green, dilated at the bases, with prominent stipule scars on the adaxial surfaces; leaf blades large, membranaceous to subcoriaceous, (15–)22–38(–60) cm. long, (6–)10–23.5 cm. wide, obovate-lanceolate, tapering to cuneate bases and acute apices, the margins entire and often undulate; upper surfaces of the blades green, glabrous; lower surfaces grayish-green, finely but thickly villous over the entire surface (particularly along the elevated, purplish or yellowish-green midveins and prominent lateral veins), the hairs ± appressed or crisped, the surfaces sometimes becoming subglabrous in age. Flowers ± vase-shaped, of disagreeable odor, held erect on stout, glabrous pedicels at the ends of branchlets, subtended by a false whorl of leaves; tepals 9 or 12, the outer 3 with broad bases, slightly shorter than the inner tepals, oblong-spatulate in outline, light greenish-white, usually reflexed at anthesis, the inner 6 or 9 creamy white, thick and fleshy, 8–12 cm. long, 2.6–4 cm. wide, obovate to oblong-elliptic in outline, tapering to narrow, ± clawed bases; stamens 1.5–2.2 cm. long, the filaments reddish, the anther sacs creamy white; gynoecia ca. 2.5 cm. long at anthesis, pinkish. Fruit aggregates ovoid-cylindric, 7–10 cm. long, green, becoming pinkish

at dehiscence, finally purplish-brown; seeds ca. 1 cm. long, the outer seed coats pinkish-red, the inner ones roughened by longitudinal grooves. $2n = 38$. (*M. umbrella* Desrouss.) — UMBRELLA-TREE, ELKWOOD.

Native to rich woods of eastern North America from southern Pennsylvania and West Virginia south into Florida (Okaloosa County) and westward through Ohio and Kentucky to Arkansas and Missouri; sometimes escaped from cultivation northward into central Massachusetts.

Magnolia tripetala has been involved in a number of hybrids, and one, *M. tripetala* × *M. sieboldii*, an intersectional hybrid, is represented in cultivation by the cultivar 'Charles Coates' (see J. R. Sealy, Gard. Chron. III. 152: 77. 1962). A tall, loosely branched shrub, 'Charles Coates' produces flowers that most closely resemble those of *M. sieboldii*. They are ± saucer-shaped, the inner tepals, 5.5–7.5 cm. long and 2–4.5 cm. wide, are ovate to broadly elliptic with short-clawed bases, and the androecium is purplish-red. However, the flowers are held erect like those of *M. tripetala*, the tepals have rumpled margins, and the leaves, which tend to be clustered in false whorls at the ends of branchlets, are broadly elliptic, 12–25 cm. long, 6.5–13.5 cm. wide, with cuneate bases and acute apices.

Magnolia thompsoniana (q.v.) is the collective epithet for hybrids between *M. tripetala* and *M. virginiana*, while *M. tripetala* × *M. hypoleuca* is discussed briefly under the latter species. Other reports of hybrids involving or suspected of involving *M. tripetala* (see J. C. McDaniel, Newsl. Am. Magnolia Soc. 11(1): 9–11. 1975) include *M. tripetala* × *M. officinalis* var. *biloba*, *M. tripetala* × *M. fraseri*, and *M. tripetala* × *M. macrophylla*, the last two hybrids being the results of intentional cross-pollinations made by P. J. Savage, Jr. The results of these hybridizations may eventually be of horticultural significance; however, the hybrids are currently of limited distribution in cultivation and are not described here, since documenting herbarium specimens have not been seen.

8. **M. hypoleuca** Siebold & Zuccarini, Abh. Math.-Phys. Acad. Wiss. München 4(2): 187. 1846; Fl. Jap. Fam. Nat. 1: 79. 1846.
FIGURE 2, a–c.

Large, widely branching deciduous trees, old specimens attaining 30 m., with silvery-gray, lenticellate bark; branchlets brittle, purplish or silvery (the periderm exfoliating in very thin, opaque sheets), with prominent leaf scars clustered in groups (the internodes very short), the groups separated by elongated internodes; terminal winter (mixed) buds large, purplish-green, glabrous. Leaves crowded into false whorls at the ends of branchlets or alternate and widely spaced on new shoots; petioles glabrous, purplish, (1–)2.5–3.5(–7) cm. long, stout, dilated at base, with prominent stipule scars on the adaxial surfaces; leaf blades large, subcoriaceous, (10–)16–45(–50) cm. long, (5.8–)9–20(–25) cm. wide, oblong-obovate, tapering to rounded, truncate, or usually broadly cuneate

bases, the apices abruptly acute or occasionally rounded, the margins entire and often undulate; upper surfaces of the blades green, glabrous; lower surfaces silvery or grayish-green, at first densely silky-pubescent over the entire surface with fine, ± appressed, crisped hairs, becoming less pubescent or subglabrous with age. Flowers cup- or saucer-shaped, heavily scented, held erect at the ends of branchlets on stout, glabrous pedicels, subtended by a false whorl of leaves; tepals 9–12, ± fleshy, the outer 3 shorter than the inner tepals, pale tan-green, sometimes tinged pinkish on the abaxial surfaces, ± oblong-spatulate in outline, with broad bases, the inner 6 or 9 tepals creamy white, elliptic to obovate in outline, tapering to relatively narrow bases, 8.5–12 cm. long, 1.5–4.5 cm. wide; stamens numerous, 1.5–2(–3) cm. long, the filaments purplish-red, the anther sacs creamy yellow; gynoecia ca. 3 cm. long at anthesis, the styles crimson. Fruit aggregates scarlet at dehiscence, finally light tan or brown, 13.5–20 cm. long, oblong-cylindric, the follicles with spreading stylar beaks or the beaks obsolete, the lowermost follicles concave and decurrent along the floral axis; seeds 8–11 mm. long, with bright red outer seed coats, the inner, black seed coats longitudinally grooved. *2n* = 38. (*M. obovata* Thunberg; *M. glauca* Thunberg, not L.) — JAPANESE WHITEBARK MAGNOLIA.

Native to altitudes of 1,800 m. in mountainous regions of the southern Kurile Islands, the Japanese islands of Hokkaido, Honshu, Shikoksu, and Kyushu, and the Ryukyu Islands. (See distribution map 86 in Y. Horikawa, Atlas of the Japanese flora, an introduction to plant sociology of East Asia. 12 pp. + *500 maps* + viii pp. + *map in pocket*. Tokyo. 1972.)

Hybrids between *Magnolia hypoleuca* and *M. sieboldii* have been given the collective name *M.* × *wieseneri*, described below, while an F_1 generation of hybrids between *M. hypoleuca*, the seed parent, and *M. virginiana*, the pollen parent, were produced in 1956 by W. F. Kosar at the United States National Arboretum. Specimens of these hybrid plants, which are apparently sterile (see Morris Arb. Bull. 20: 65. 1969), are almost indistinguishable from specimens of *M.* × *thompsoniana* (q.v.), and they would be traced to that hybrid group in the key presented in this treatment. While these hybrids are not yet in cultivation other than at the National Arboretum, a cultivar selected from the plants is expected to be distributed to nurseries for propagation in the near future. Likewise, *M. hypoleuca* × *M. fraseri* and *M. hypoleuca* × *M. macrophylla* have been produced as the results of intentional cross-pollinations by P. J. Savage, Jr., a noted *Magnolia* authority (see J. C. McDaniel, Newsl. Am. Magnolia Soc. 11(1): 9–11. 1975). These hybrids are not known by me to be grown outside of the collections of a few *Magnolia* specialists and hybridizers, and I have not seen documenting herbarium specimens.

Another hybrid, involving *Magnolia hypoleuca* and the closely related *M. tripetala*, has been reported as occurring spontaneously in cultivation in Poland (see E. V. Vašák, Newsl. Am. Magnolia Soc. 9(1): 3–6. 1973).

A large tree upwards of 10 m., with the habit of *M. hypoleuca* and growing in the Arnold Arboretum (Accession #1280–27–C), is also undoubtedly *M. hypoleuca* × *M. tripetala.* Despite its overall resemblance to *M. hypoleuca*, the putative hybrid can be distinguished from that species by its more nearly elliptic leaf blades, its flowers intermediate between those of the two parents, and its fruit aggregates, which agree almost exactly with those of *M. tripetala.* The Arnold Arboretum plant was grown from seed collected from an Arboretum plant of *M. hypoleuca* (Accession #15172; now dead) that was growing in close association with *M. tripetala.* The seed parent, in turn, had been grown from seed of *M. hypoleuca* collected in Japan by C. S. Sargent in 1892.

9. **M. officinalis** Rehder & Wilson, Pl. Wilsonianae 1: 391. 1913.

Deciduous trees to 20 m., very similar to *Magnolia hypoleuca*; bark rusty ash-gray, the stout branchlets yellowish or yellowish-gray, finally light gray, becoming longitudinally striate when dried, the prominent leaf scars clustered in groups (the internodes very short), the groups separated by elongated internodes; periderm exfoliating in thin sheets; terminal winter (mixed) buds large, greenish-brown, glabrous. Leaves large, clustered in false whorls at the ends of branchlets or alternate and widely spaced on new shoots; petioles glabrescent, stout, 2.5–3.8(–4) cm. long, yellowish-green, dilated at base, with conspicuous stipule scars on the adaxial surfaces; leaf blades membranaceous to subcoriaceous, (10–) 22–40 cm. long, (5.5–)11–20 cm. wide, oblong-obovate, tapering to rounded, acute, or usually cuneate bases, the apices rounded to abruptly acute, the margins entire, undulate; upper surfaces of the blades green, glabrous; lower surfaces silvery or grayish-green, at first densely felted over the entire surface with fine, ± appressed, crisped hairs, the lamina becoming subglabrous but distinctly glaucous. Flowers heavily scented, held erect at the ends of branchlets on stout, glabrous to silky-pubescent or felted pedicels, subtended by a false whorl of leaves; tepals 9–12(–17), ± thick and fleshy, the outer 3 subequal to the inner tepals, oblong-spatulate, pale greenish-white, often tinged with pink on the abaxial surfaces, becoming reflexed during anthesis, the inner 6–9(–14) tepals creamy white, obovate to spatulate, 8–10 cm. long, 2.5–4.4 cm. wide, tapering to relatively narrow, ± clawed bases; stamens ca. 1.5 cm. long, with reddish filaments and creamy yellow anther sacs; gynoecia 2.5–3 cm. long at anthesis, the stigmas reddish. Fruit aggregates red at dehiscence, finally reddish- or purplish-brown, 9–15 cm. long, oblong-ovoid, with obtuse to ± acute apices, the follicles with short, spreading stylar beaks; lowermost follicles rounded (convex) at base, not decurrent along the floral axis; seeds ca. 1 cm. long, with red outer seed coats, the inner seed coats black, longitudinally grooved. $2n = 38$.

Apparently once native to a wide area of Central China, where it is now thought to persist only as a cultivated plant. Rehder and Wilson

comment that individuals of this species have been eliminated from natural habitats owing to the collection of its bark, which is of reputed medicinal value.

The differences between *Magnolia officinalis* and the Japanese *M. hypoleuca* are few and largely subjective. It is probable that the Chinese plants should be treated at a subspecific rank under *M. hypoleuca*. I have not, however, seen enough material on which to base such a transfer and change in rank, and *M. officinalis* is therefore maintained here provisionally as a species. My observations indicate that the only consistent difference between *M. officinalis* and *M. hypoleuca* is the attitude of the basal follicles of the mature fruit aggregates. The basal follicles of *M. hypoleuca* are concave and decurrent along the floral axis, giving the aggregate an attenuate base, while the lowermost follicles of *M. officinalis* are convex and not decurrent along the axis below, giving the aggregate a rounded base. While the pedicels of *M. hypoleuca* are consistently glabrous, those of the majority of specimens of *M. officinalis* examined are densely pubescent at anthesis. Yet one or two collections of *M. officinalis*, including the type collection (*Wilson 652*), represent plants in flower with both pubescent and glabrous pedicels. Likewise, the pubescence of immature petioles (usually pubescent in *M. officinalis* and glabrous in *M. hypoleuca*) is not a sound character on which to distinguish the two taxa. The branchlets of *M. officinalis* are yellowish-gray and become longitudinally striate when prepared as herbarium specimens. Branchlets of *M. hypoleuca* are purplish- or silvery-brown and, it would appear, fail to become striate when dried.

Plants of *Magnolia officinalis* with all or the great majority of the leaves emarginate at the apex have been described as var. *biloba* Rehder & Wilson, Pl. Wilsonianae 1: 392. 1913 (= cv. Biloba; *M. biloba* (Rehder & Wilson) Cheng [2]), and this variety also probably occurs today only as a cultivated plant. Rehder and Wilson state that var. *biloba* agrees with var. *officinalis* in all features except the character of the leaf apex, and Johnstone (1955), in suggesting that the recognition of var. *biloba* is tenuous, states that bilobed leaves occasionally occur on plants of var. *officinalis*. However, my observations indicate that the stipular scales enclosing terminal buds on branchlets of var. *biloba* are consistently pubescent with rufous hairs on the outer surfaces, while the inner surfaces are densely felted with these hairs. In both var. *officinalis* and *M. hypoleuca* the corresponding scales are glabrous. This type of pubescence, together with other morphological characters, suggests the close relationship of these three taxa with *M. rostrata* W. W. Smith, Notes Roy. Bot. Gard. Edinburgh 12: 213. 1920 (excluding the description of flowers),

[2] *Magnolia officinalis* var. *biloba* was proposed as a distinct species by Cheng in Iconographia Cormophytorum Sinicorum 1: 787. 1972. The basionym for this combination is not given, suggesting that this reference may not be the original publication of the combination by Cheng. Efforts to locate an earlier reference in the Chinese literature, however, have not been successful.

another species (rare in cultivation in warmer temperate climates) with which, in the absence of mature fruit aggregates, both *M. hypoleuca* and *M. officinalis* may be confused.

MAGNOLIA sect. OYAMA Nakai, Fl. Sylv. Koreana 20: 117. 1933.

Small deciduous trees or shrubs; flowers nodding or pendent; stamens reddish, with blunt or rounded apices; fruit aggregates pendent. TYPE SPECIES: *M. sieboldii* Sieb. & Zucc.

As accounted for here, including three eastern Asiatic species, one comprised of two subspecies, all known in cultivation in western gardens.

10. **M. globosa** J. D. Hooker & T. Thomson, Fl. Indica 1: 77. 1855.
FIGURE 3, 1.

Deciduous shrubs or small trees to ca. 7 m., usually of wide-spreading habit; branchlets slender to ± stout, reddish-brown or dark reddish-purple, at first densely felted with rufous pubescence, eventually glabrous; terminal winter (mixed) buds densely rufous-pubescent to nearly glabrous. Petioles 2.5–4(–5.5) cm. long, densely sericeous with silvery, yellowish, or rufous hairs, sometimes becoming subglabrous in age, the elongate stipule scars on the adaxial surfaces extending more than half the lengths of the petioles; leaf blades elliptic, broadly ovate, oblong-ovate, or usually obovate, (6–)–21(–23) cm. long, (4.5–)7–9(–14.5) cm. wide, with acute to ± rounded apices, entire margins (usually ciliate when young), and acute or usually rounded or subcordate, sometimes ± truncate bases; upper surfaces of the blades glossy dark green, with short, crisped hairs along the midveins and major lateral veins, otherwise glabrous; lower surfaces glaucous, finely pubescent over the entire surface with ± appressed, crinkled hairs; when immature and expanding, the lower surfaces with dense, felted or woolly, rufous, yellowish, or silvery pubescence along the midveins and major lateral veins, this pubescence sometimes persisting. Flowers fragrant, creamy white, cup-shaped or subglobose, appearing with the leaves, pendent or nodding on stout, rufous-pubescent pedicels (3.5–)4.5–6.5 cm. long; tepals 9–12, the outer whorl of 3 similar in size and shape to the inner tepals, the inner tepals spatulate to obovate or elliptic, with rounded apices, 4–7(–7.5) cm. long, 2–3 cm. wide; stamens 12–17 mm. long, reddish-purple; gynoecia ca. 3.5 cm. long at anthesis, greenish. Fruit aggregates pinkish at dehiscence, finally reddish-brown, cylindric, 6–8 cm. long, with curving stylar beaks; seeds ca. 7 mm. long, the outer seed coats red. $2n = 38$. (*M. tsarongensis* W. W. Smith & G. Forrest.)

Native to a wide area from eastern Nepal, Bhutan, and northeastern Assam to southeastern Tibet, northern Burma, and western China (northwestern Yunnan Province).

For *Magnolia wilsonii* × *M. globosa*, see under *M. wilsonii*.

FIGURE 3. **Magnolia** sect. **Oyama.** a–g, *M. sieboldii* subsp. *sieboldii*: a, flower bud, × ½; b, flower, × ½; c, adaxial view of stamen showing lines of anther sac dehiscence and blunt apex, × 3; d, abaxial view of stamen, × 3; e, outline of typical leaf, × ⅓; f, fruit aggregate, × ½; g, seeds, the outer seed coats removed, × 1. h, i, *M. sieboldii* subsp. *sinensis*: h, habit of flowering branchlet, × ⅓; i, outline of typical leaf, × ⅓. j, k, *M. wilsonii*: j, outline of typical leaf, × ⅓; k, fruit aggregate, × ½. l, *M. globosa*, outline of typical leaf, × ⅓.

11. **M. wilsonii** (Finet & Gagnepain) Rehder, Pl. Wilsonianae 1: 395. 1913. FIGURE 3, j, k.

Deciduous shrubs or small trees to ca. 8 m., often of ± straggling habit, the brownish bark with conspicuous corky lenticels; branchlets slender, dark reddish-purple, becoming dark grayish-purple, at first dense-

ly sericeous with rufous hairs, eventually glabrous; terminal winter (mixed) buds greenish-brown, thinly to densely pubescent with rufous hairs. Petioles slender, (0.4–)1–3(–4) cm. long, densely sericeous with rufous hairs, becoming less so in age, the elongate stipule scars on the adaxial surfaces extending more than half the lengths of the petioles; leaf blades elliptic or usually lanceolate to oblong-ovate, (4–)6.5–15.5 (–20) cm. long, (2.5–)3–7(–11) cm. wide, with truncate or rounded, rarely cuneate or acute bases, entire margins (sometimes ciliate when young), and acute to acuminate apices; upper surfaces of the blades green, at first with scattered hairs along the midveins and major lateral veins, otherwise glabrous; lower surfaces thickly felted to thinly sericeous over the entire surface (when felted, the hairs obscuring the glaucous lamina), the hairs along the often obscured midveins and major lateral veins yellowish or rufous, the other hairs silvery-gray, without pigment deposition in the crosswalls. Flowers fragrant, cup-shaped at first, becoming saucer-shaped, appearing with the leaves, pendent on slender, ± sericeous pedicels 1.5–4.5 cm. long; tepals 9 or occasionally 12(–16), the outer 3 subequal to the inner tepals, narrowly lanceolate to spatulate, with acute to rounded apices and tapering to relatively broad bases, the inner tepals pure white, 4–6.5(–7.5) cm. long, 3–4.5(–5.5) cm. wide, in outline broadly spatulate to obovate or suborbicular, with rounded apices and short-clawed bases; stamens 9–12 mm. long, rosy-purple; gynoecia ca. 2 cm. long at anthesis, greenish. Fruit aggregates pendent, pinkish at dehiscence, becoming purplish-brown, cylindric, (5.5–)6–10 cm. long, with spreading stylar beaks; seeds ca. 6 mm. long, the outer seed coats red. $2n = 38$. (*M. parviflora* var. *wilsonii* Finet & Gagnepain; including *M.* × *highdownensis* Dandy = *M. wilsonii* × *M. sieboldii* subsp. *sinensis*, as *M. sinensis*.) — WILSON'S MAGNOLIA.

Native to eastern Sikang, western Szechwan, and northern Yunnan provinces, China, where it has been collected at altitudes between 1,900 and 3,300 m.

Plants with the leaves decidedly glaucous on the lower surfaces of the blades and, except for the rufous-pilose midveins, sparsely appressed-pubescent or glabrescent have been recognized as f. *nicholsoniana* (Rehder & Wilson) Rehder, Jour. Arnold Arb. 20: 91. 1939 (*M. nicholsoniana* Rehder & Wilson; *M. taliensis* W. W. Smith; *M. wilsonii* f. *taliensis* (W. W. Smith) Rehder). This form was discovered by E. H. Wilson in the vicinity of Wa-shan, in western Szechwan Province.

One specimen of *Magnolia wilsonii* examined, *Williams s.n.* (AAH), consists of what appears to be a double-flowered form with 15 or 16 tepals. This collection was made from a plant grown at Wakehurst Place, Sussex, England; the plant is also referred to by Johnstone (1955, p. 125). It is not known, however, whether this or similar forms of *M. wilsonii* have been introduced into American gardens.

Putative hybrids between *Magnolia wilsonii* and *M. sieboldii* subsp. *sinensis* (as *M. sinensis*) have received the collective name *M.* × *high-*

downensis Dandy, Jour. Roy. Hort. Soc. 75: 159. *fig. 82*. 1950 (see also F. C. Stern, New Flora & Silva 10: 105–107. *fig. 33*. 1938). However, clonal plants of this putative hybrid that I have seen growing in England fall into the range of variation encountered in *M. wilsonii* and are similar to specimens of *M. wilsonii* collected in China. As a result, the name *M.* × *highdownensis* is placed in the synonymy of *M. wilsonii*.

An intentional interspecific hybrid, *Magnolia wilsonii* × *M. globosa*, has been produced as the result of deliberate cross-pollinations (see D. T. Gresham, Morris Arb. Bull. 17: 70–73. 1966). This hybrid is not described here, because I have not seen documenting herbarium specimens; nor do I have any record that the hybrids (F_1 generation) are grown within our area.

12. **M. sieboldii** K. Koch, Hort. Dendrol. 4. 1853. FIGURE 3, a–i.

Small deciduous trees to 10 m. or often large shrubs with several trunks from the base; branchlets slender, yellowish- or silvery-tan, sometimes becoming reddish-brown on exposed surfaces, at first thickly appressed-sericeous with silvery or ± rufous hairs or rarely subglabrous, eventually glabrous; terminal winter (mixed) buds finely appressed-pubescent to densely villous with tan or rufous hairs. Petioles slender, (0.8–)1.3–4.5(–5.5) cm. long, appressed-sericeous with silvery or sometimes rufous hairs, the stipule scars on the adaxial surfaces extending about half the lengths of the petioles, rarely longer; leaf blades elliptic, broadly elliptic, ovate, or characteristically broadly obovate, (5.5–)9–12(–16) cm. long, (3.4–)5.5–9.7 cm. wide, with broadly cuneate, rounded, ± truncate, or rarely subcordate bases, entire margins (sometimes ciliate when young), and acute to abruptly acute or short-acuminate apices; upper surfaces of the blades green, often with few, short hairs along the depressed midveins and prominent lateral veins, otherwise glabrous; lower surfaces of the blades glaucescent, rarely ± glabrescent, usually densely sericeous along the elevated midveins and major lateral veins when young and finely sericeous over the entire surface, the hairs ± straight, at least some or occasionally all with rusty-red pigment in the crosswalls. Flowers fragrant, cup-shaped at first, becoming ± saucer-shaped, appearing with the leaves, held nodding or ± pendent on slender, pubescent pedicels (2.5–)3–6(–7) cm. long; tepals 9–12, pure white, the outer 3 subequal to the inner ones, the inner tepals spatulate to broadly obovate, with rounded apices and cuneate to short-clawed bases, 3.5–6 cm. long, 2–4.4 cm. wide; stamens numerous, 10–15 mm. long, reddish-purple; gynoecia greenish, ca. 1.5 cm. long at anthesis. Fruit aggregates ± pendent, pinkish at dehiscence, becoming dark purplish-brown, cylindric, 2–7 cm. long, with short, ± erect stylar beaks; seeds ca. 6 mm. long, the outer seed coats red. $2n = 38$. (*M. parviflora* Sieb. & Zucc., not Blume; *M. verecunda* Koidzumi.)

Native to a wide area of eastern Asia in Japan, Korea, and Manchuria; also known disjunctly from Anwhei and Kwangsi [3] provinces, China.

Plants with the young branchlets tomentose with yellowish or ± rufous hairs, occasionally larger leaf blades to 21.5 cm. long and 15.9 cm. wide (some ± suborbicular), longer petioles to 6.4 cm. long, the stipule scars extending more than half the lengths of the petioles, and hairs on the lower surfaces of the leaf blades ± appressed and crinkled, lacking red or rust-colored pigment in the crosswalls are recognized here as **Magnolia sieboldii** subsp. **sinensis** (Rehder & Wilson) Spongberg, comb. et stat. nov. (BASIONYM: *Magnolia globosa* Hooker f. & Thompson var. *sinensis* Rehder & Wilson, Pl. Wilsonianae 1: 393. 1913; syn. *M. sinensis* (Rehder & Wilson) Stapf, Bot. Mag. 149: *sub t. 9004*. 1924; *M. nicholsoniana* Hort., **not** Rehder & Wilson).

This subspecies is apparently endemic to a small area of northwestern Szechwan Province, China, where the type specimens, *Wilson 1422* (A, five sheets!; K, three sheets!), were collected west of and near Wen-ch'uan at 2,000 to 2,600 m. by E. H. Wilson in June and September of 1908. First proposed as a variety of *Magnolia globosa*, subsp. *sinensis*, $2n = 38$, has been recognized by most authors as a distinct species closely related to both *M. globosa* and *M. wilsonii*. However, during this study it was concluded that the closest affinities of the Szechwan plants are with *M. sieboldii* and that this relationship is best reflected by treating the taxon as a subspecies of *M. sieboldii*. This conclusion became inevitable when a comparison was made between one collection of *M. sieboldii* subsp. *sieboldii* from a plant cultivated on Martha's Vineyard, Massachusetts, *Spongberg & Hill 74–14* (AAH), and the flowering specimens constituting the type collection of *M. globosa* var. *sinensis*. The flowering specimens of these two collections could well have come from a single gathering. Only after an examination and comparison of these collections with a series of specimens of *M. sieboldii* subsp. *sieboldii* (of both spontaneous and cultivated origin) were differences noted which distinguish the two taxa. The fact that subsp. *sieboldii* is wide-ranging in nature while subsp. *sinensis* is widely disjunct and apparently restricted to a small area of northwestern Szechwan Province suggests that the species once was more widely distributed and that the Szechwan population(s) has become morphologically differentiated as a result of geographic isolation.

Magnolia × *wieseneri* (q.v.) is a hybrid between *M. sieboldii* and *M. hypoleuca* occasionally cultivated in western gardens and arboreta, while *M. sieboldii* × *M. tripetala* is represented in cultivation by the cultivar 'Charles Coates', described briefly under *M. tripetala*.

[3] I have been unable to locate any earlier mention of the occurrence of *Magnolia sieboldii* in Kwangsi Province. It is credited here to that province on the basis of two specimens, *Z. S. Chung 82074*, Chuen Yuen, June 20, 1937 (A), and *Z. S. Chung 83515*, **without precise locality or date** (A).

MAGNOLIA subg. YULANIA (Spach) Reichenbach, Rep. Herb. Nomencl. Gen. Pl. (Deutsche Bot.) 1(1): 192. 1841.

Deciduous trees and shrubs; flowers precocious or appearing with the leaves; tepals subsimilar or the outer whorl reduced in size and sepaloid; anther sacs laterally or sublaterally dehiscent.

Three sections, one with species in eastern North America and eastern Asia, two with species restricted to eastern Asia.

KEY TO THE SPECIES AND SELECTED HYBRIDS OF MAGNOLIA SUBG. YULANIA IN CULTIVATION

1. Tepals subequal, the outer whorl petaloid, not simulating a calyx; flowers precocious, sometimes continuing to flower as the leaves expand; tepals white to purple. ..... 2.
   2. Tepals (12–)15–33, narrowly oblong or strap-shaped, 0.6–1.4(–1.7) cm. wide. ..... 20. *M. kobus* var. *stellata*.
   2. Tepals (5–)6–12(–16), spatulate to obovate or oblanceolate, (1.4–)2.5–7.5(–8) cm. wide. ..... 3.
      3. Tepals of the innermost whorl held erect, connivent, enclosing the androecium and gynoecium, the outer whorls held ± horizontally or occasionally reflexed; leaf blades generally elliptic to oblong-ovate, with 12 or more pairs of major lateral veins. ..... 4.
         4. Tepals 12–16; fruit aggregates 11–15(–20) cm. long; upper surfaces of the leaf blades glabrous. ..... 13. *M. campbellii*.
         4. Tepals 7–10; fruit aggregates 7–10 cm. long; upper surfaces of the leaf blades with short hairs along the veins. 26. *M.* × *veitchii*.
      3. Tepals of the innermost whorl not connivent, not enclosing the androecium and gynoecium, the outer whorls held ± horizontally or drooping; leaf blades generally obovate to oblanceolate, with 12 or fewer pairs of major lateral veins. ..... 5.
         5. Flowers held ± erect on the branchlets; leaves usually obovate to oblanceolate, apically acute or usually abruptly short-acuminate. ..... 6.
            6. Tepals or tepal scars 9, the tepals tapering downward to broad bases. ..... 7.
               7. Flowers precocious; tepals white, the outer whorl subequal to the inner whorls. ..... 14. *M. heptapeta*.
               7. Flowers precocious, sometimes continuing until after the leaves have expanded; tepals rarely white throughout, the abaxial surfaces usually flushed pink to dark purple, the outer whorl of tepals often ca. half as long as the inner tepals. ..... 27. *M.* × *soulangiana*.
            6. Tepals or tepal scars 12 or more, the tepals tapering downward to relatively narrow, ± clawed bases. ..... 8.
               8. Tepals rosy-red on the abaxial surfaces; leaves generally less than twice as long as broad. ..... 15. *M. sprengeri* var. *sprengeri*.
               8. Tepals white on the abaxial surfaces; leaves generally more than twice as long as broad. 15. *M. sprengeri* var. *elongata*.

5. Flowers held ± horizontally on the branchlets; leaves usually obovate to oblanceolate, with rounded or sometimes emarginate apices. ..... 9.
9. Tepals (10–)12–16, purplish-pink on the abaxial surfaces; leaf blades finely reticulate, the lower surfaces finely pubescent over the lamina or adjacent to the midveins. .. 10.
10. Tepals 12–14, 6.4–9 cm. long; leaf blades generally less than twice as long as broad. ..... 16. *M. sargentiana* var. *sargentiana*.
10. Tepals 10–16, 8.4–12.5 cm. long; leaf blades generally more than twice as long as broad. ..... 16. *M. sargentiana* var. *robusta*.
9. Tepals 9–12, pale pink on the abaxial surfaces; leaf blades strongly reticulate, the lower surfaces glabrous or with few, scattered hairs along the veins. ... . 17. *M. dawsoniana*.

1. Tepals very unequal, the outer whorl sepaloid, simulating a calyx, sometimes caducous; flowers precocious or appearing with the leaves; petaloid tepals white, purplish, greenish, or yellowish. ..... 11.
11. Flowers precocious; petaloid tepals white, sometimes flushed pink to purple at the base, or the tepals pink to purple. ..... 12.
12. Flowers often continuing after the leaves have expanded; petaloid tepals flushed pink to purple on the abaxial surfaces, white to pink or purplish within. ..... 13.
13. Shrubs; flowers continuing to appear with the leaves; stipule scars extending almost to the base of the blades, the lamina often decurrent along the petiole; leaf blades with hairs along the midveins or glabrous beneath. ..... 21. *M. quinquepeta*.
13. Large shrubs or usually trees; flowers primarily precocious, some flowers appearing with the leaves; stipule scars small, basal, the lamina not decurrent along the petiole; leaf blades usually puberulent over the lower surfaces. ..... 27. *M.* × *soulangiana*.
12. Flowers not continuing after the leaves have expanded; petaloid tepals white on both surfaces, sometimes tinged pink to purple basally, rarely with the abaxial surfaces flushed pink throughout. 14.
14. Petaloid, inner tepals (5–)6–16, spatulate, obovate or oblanceolate, (1.4–)2–4.5 cm. wide, the outer whorl of sepaloid tepals persistent at anthesis; young branchlets glabrous or finely sericeous. ..... 15.
15. Lower surfaces of the leaf blades finely puberulent over the entire surface or at least adjacent to the midveins. 16.
16. Flowers held ± erect on the branchlets; petaloid tepals 6, ± erect; branchlets finely sericeous. ..... 18. *M. cylindrica*.
16. Flowers held ± horizontally on the branchlets; petaloid tepals 6, rarely to 12, ± drooping; branchlets glabrous. ..... 19. *M. salicifolia*.
15. Lower surfaces of the leaf blades glabrous or with long hairs scattered along the veins and/or in the axils of the midveins and major lateral veins. ..... 17.
17. Petaloid tepals (5)6 or 7. 20. *M. kobus* var. *kobus*.

17. Petaloid tepals (11)12–16. ..... 20. *M. kobus* var. *loebneri.*

14. Petaloid tepals (12–)15–33, narrowly oblong or strap-shaped, 0.6–1.4(–1.7) cm. wide, the outer whorl of sepaloid tepals often caducous or sometimes abortive; young branchlets finely sericeous. ..... 20. *M. kobus* var. *stellata.*

11. Flowers appearing with the expanded leaves; tepals purplish, greenish, or yellowish. ..... 18.

18. Large shrubs; petaloid tepals purplish. ..... 21. *M. quinquepeta.*

18. Large trees or rarely shrubs; petaloid tepals greenish to golden yellow. ..... 19.

19. Branchlets of the current and previous year glabrous; pedicels glabrous or rarely villous; tepals greenish-yellow throughout or sometimes golden yellow on the adaxial surfaces. ..... 22. *M. acuminata* var. *acuminata.*

19. Branchlets of the current and previous year with short hairs or roughened by hair bases; pedicels villous or rarely glabrous; tepals light yellow on the abaxial surfaces, golden yellow within, rarely greenish-yellow throughout. ..... 22. *M. acuminata* var. *subcordata.*

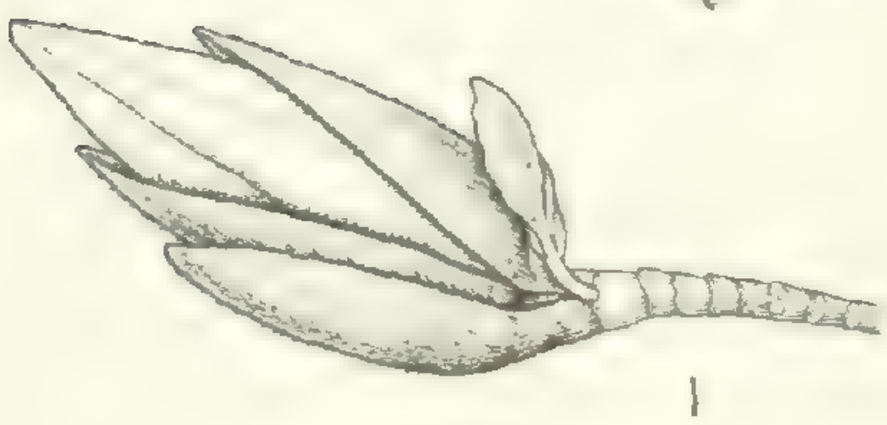
MAGNOLIA sect. YULANIA (Spach) Dandy, Camellias and Magnolias, Roy. Hort. Soc. Conf. Rep. 72. 1950.

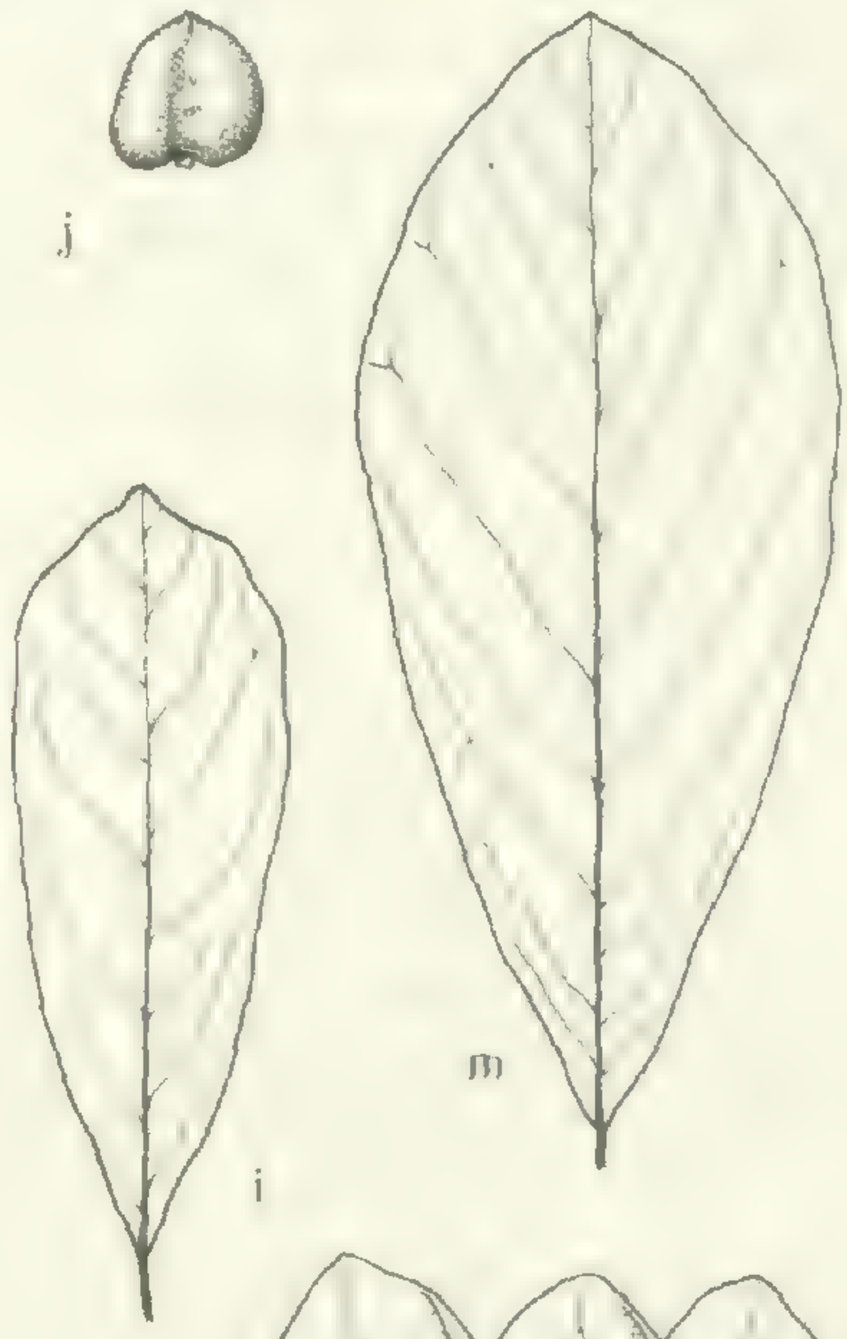
Deciduous trees and shrubs; flowers precocious; tepals subsimilar, not differentiated into an outer, sepaloid whorl and inner, petaloid whorls. TYPE SPECIES: *M. heptapeta* (Buc'hoz) Dandy (syn. *M. denudata* Desrouss.).

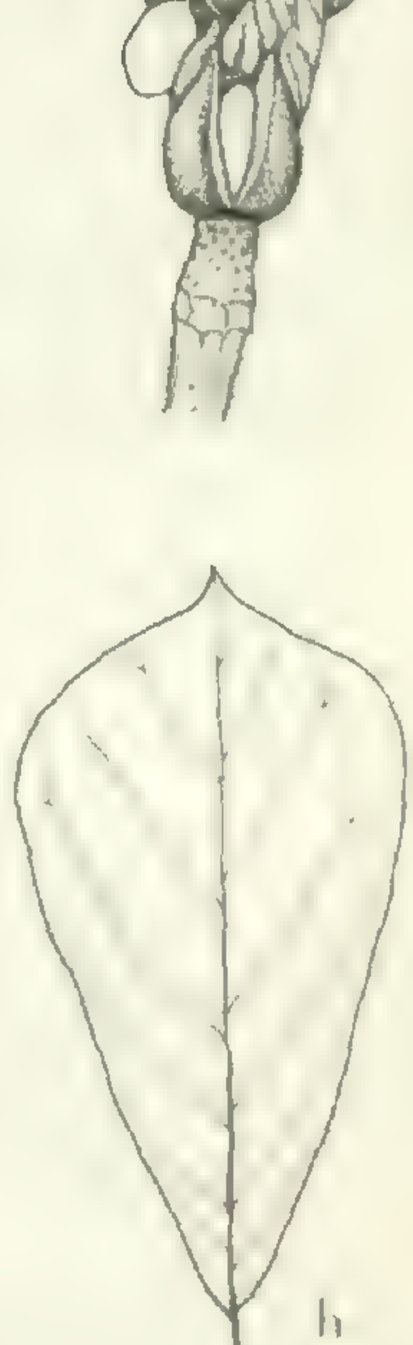
More than seven species, all of eastern Asiatic distribution, of which five are known in cultivation. Although the section is well defined, species of sect. YULANIA are in need of more study. Despite importation of limited quantities of seed, several species of the section are variable in cultivation. Because knowledge of several of these species in nature is based on limited herbarium material (in some instances only the type collections), it is to be expected that further knowledge of variation in nature might result in taxonomic changes.

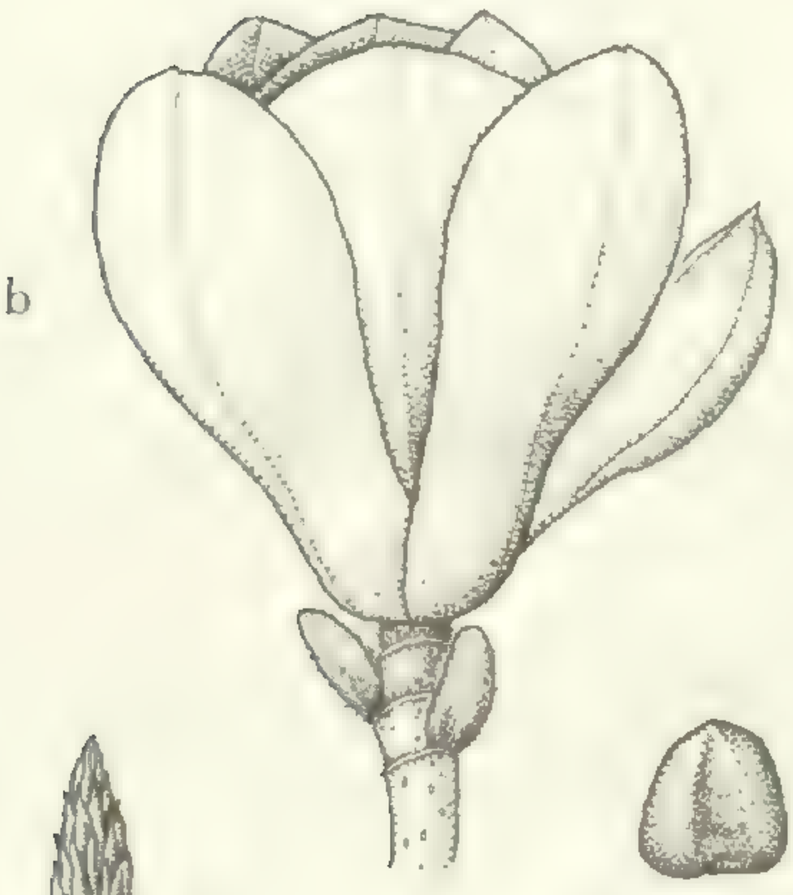
13. **M. campbellii** J. D. Hooker & T. Thomson, Fl. Indica 1: 77. 1855. FIGURE 4, a.

Large deciduous trees with grayish-tan bark, often with several boles from near the base, in nature to 30 (or 45?) m., or occasionally large shrubs (*fide* G. Forrest); branchlets slender to ± stout, yellowish-green or greenish-tan, becoming dark reddish-brown, glabrous, lenticellate; terminal winter (mixed) buds ovoid, finely sericeous to densely woolly with yellowish-white hairs, the vegetative buds finely sericeous or subglabrous. Leaves variable, subcoriaceous, the petioles (0.8–)1–5 cm. long, glabrous, finely pubescent, or occasionally finely pubescent only at the distal end, with small basal stipule scars on the adaxial surfaces; leaf









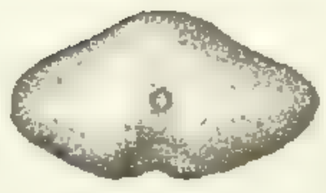


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FIGURE 4. **Magnolia** sect. **Yulania.** a, flower of *M. campbellii* with connivent inner tepals, × ⅓. b–f, *M. heptapeta*: b, flower, × ½; c, flower with tepals removed to show the androecium and gynoecium, × ¾; d, adaxial view of stamen, × 1½; e, lateral view of stamen showing lateral line of anther sac dehiscence, × 1½; f, fruit aggregate, × ½. g–k, *M. sprengeri*: g, terminal winter (mixed) bud, × ½; h, outline of typical leaf of var. *sprengeri*, × ⅓; i, outline of typical leaf of var. *elongata*, × ⅓; j, seed with outer seed coat removed, × 1; k, view of micropylar end of seed showing basal pore with stalk, × 2. l–o, *M. sargentiana*: l, terminal floral bud enclosed by spathaceous stipular bracts, × ⅓; m, outline of typical leaf, × ⅓; n, seed with the outer seed coat removed, × 1; o, view of micropylar end of seed showing basal pore, × 2. p, habit of flowering branchlet of *M. dawsoniana*, × ⅓.

blades (8–)11.5–23.5(–33.5) cm. long, (3.8–)4.6–10.7(–14.5) cm. wide, elliptic, oblong-ovate or broadly obovate to oblong-oblanceolate, with acute to short-acuminate apices and rounded to cuneate, often unequal bases; upper surfaces of the blades dark green, reticulate, glabrous; lower surfaces pale green, completely glabrous, finely velutinous along the midveins and major lateral veins or finely appressed-sericeous over the entire surface with silvery hairs. Flowers large, faintly fragrant, precocious, held erect on stout, glabrous or sometimes pubescent pedicels ca. 2 cm. long; tepals 12–16, deep to pale crimson or pink on the abaxial surfaces, the inner surfaces suffused with the same color, or the tepals pure white, the outer whorls held ± horizontally or occasionally reflexed and drooping, the tepals concave, broadly spatulate to oblong-ovate, usually constricted basally into a short claw, (6.5–)9.5–14 cm. long, (2.2–)4.2–6.2 cm. wide, the innermost whorl held erect, connivent, enclosing the androecium and gynoecium, these tepals broadly obovate to subglobose, clawed at base, (7.7–)8.5–10.3 cm. long, (3.5–)4.3–6 cm. wide; stamens numerous, (1–)1.5–3 cm. long, the filaments purplish-red; gynoecia 2–3 cm. long at anthesis, the carpels glabrous or finely sericeous, greenish, the stigmas reddish. Fruit aggregates held erect, eventually pendulous, cylindric, (7.5–)11–15(–20) cm. long when fully developed, often asymmetrical and/or shorter from seed abortion, dull pinkish-red at dehiscence, finally brownish, the follicles indiscrete prior to dehiscence; seeds ca. 1 cm. long, the outer seed coats red, the inner seed coat with a small basal pore. $2n = 114$.

A variable species, spectacular in bloom, native to a wide area of the Himalayan region from eastern Nepal through Bhutan, northern Assam, southeastern Tibet, and Upper Burma into Yunnan Province, China; unfortunately, hardy only in the milder areas of our range.

Plants of this species in cultivation are apparently derived primarily from seed collected at the two ends of the range, i.e., Sikkim and Yunnan (Johnstone, 1955, p. 47). George Forrest's collections from the eastern end of the range, mostly from the vicinity of the Shweli-Salwin Divide, were originally proposed as a distinct species, *Magnolia mollicomata* W. W. Smith, Notes Roy. Bot. Gard. Edinburgh 12: 211. 1920, but J. E. Dandy (*Ibid.* 16: 123, 124. 1928) later pointed out that the eastern and western plants were linked by intermediate populations in the intervening range, and on this basis he submerged *M. mollicomata* within *M. campbellii*. However, recognition of the Yunnan plants at some rank under *M. campbellii* may be justified, since they can usually be distinguished by their densely yellowish-sericeous or felted pedicels, their branchlets with persistent pubescence along one or two internodes beneath terminal stipular bud scale scars, and their elongate mixed (floral) buds. In cultivation, the Yunnan plants grown from Forrest's seed collections, while variable, are hardier than typical *M. campbellii* and commence to produce flowers at an earlier age. Although a larger series of specimens than I have seen from native habitats will be required to assess

and fully understand the variation of *M. campbellii* over its wide range, those plants from the eastern end of that area with the above mentioned characteristics have previously been recognized under *M. campbellii* as var. *mollicomata* (W. W. Smith) F. Kingdon-Ward, Gard. Chron. III. 137: 238. 1955, or as *M. campbellii* subsp. *mollicomata* (W. W. Smith) Johnstone, Asiatic Magnolias Cult. 53. 1955.

Like other species of sect. YULANIA, numerous plants of *Magnolia campbellii* grown from imported Asian seed or seed collected from plants grown in western gardens have proven variable in flower size, shape, and color, in leaf size, shape, and pubescence, and in their period of blooming. Owing to the great beauty of several distinctive plants in cultivation, they have been given cultivar names; reference should be made to Fogg and McDaniel (1975) for a listing of the cultivars and to D. T. Gresham (Morris Arb. Bull. **15**: 29–31. 1964) and E. McClintock (Jour. Calif. Hort. Soc. 23: 30–36. 1962) for more detailed information concerning a number of these variants.

Magnolia × *veitchii* (q.v.) is the collective epithet for hybrids between *M. campbellii* and *M. heptapeta*. Crosses between the two varieties of *M. campbellii*, sometimes referred to as *M.* × *raffillii*, an illegitimate name (see N. G. Treseder, Newsl. Am. Magnolia Soc. **5**: 7. 1968), have also been produced and are represented in cultivation by the cultivars 'Charles Raffill' (see Jour. Roy. Hort. Soc. **88**: 494. *figs. 173, 174.* 1973) and 'Kew's Surprise' (*Ibid.* **92**: 235. 1967). Trihybrids between *M. campbellii* and *M.* × *soulangiana* have been produced in England but are known to me in cultivation in North America only outside our range, at the Strybing Arboretum. Furthermore, the cultivar 'Caerhays Surprise' (see F. J. Williams, Jour. Roy. Hort. Soc. **99**: 364, 365. *fig. 173.* 1974) represents the results of intentional hybridization between *M. campbellii* (as var. *mollicomata*) and *M. quinquepeta* 'Nigra' (as *M. liliflora*). This hybrid is not known by me to be grown in the United States.

14. M. heptapeta (Buc'hoz) J. E. Dandy, Jour. Bot. 72: 103. 1934.
FIGURE 4, b–f.

Twiggy deciduous trees to ca. 15 m., usually of ± rounded habit, or occasionally large shrubs; bark dark gray, rough and fissured; branchlets stout, lenticellate, finely to densely sericeous, soon glabrous, reddish- or purplish-brown, eventually silvery-gray; vegetative buds finely pubescent, the terminal winter (mixed) buds densely sericeous with silvery-gray or yellowish hairs. Petioles 1.3–2 cm. long, finely tomentose, with small basal stipule scars on the adaxial surfaces; leaf blades membranaceous, 6.5–13.5(–15) cm. long, 4.6–8.5(–11.2) cm. wide, rarely elliptic or broadly obovate to subrounded, usually obovate to oblong-obovate, tapering to cuneate, obtuse, or subrounded, rarely ± truncate bases, the distal ends ± rounded or truncate, usually produced into abruptly short-acuminate apices, the margins entire; upper surfaces of the blades dark green, ± reticulate, sparingly pubescent along the major veins, oc-

casionally along the secondary veins; lower surfaces ± reticulate, light green, puberulent along the veins. Flowers lemony-fragrant, precocious, ± vase-shaped, held erect on short, densely yellowish-villous pedicels; tepals 9 (or rarely 12), subsimilar, white or ivory, sometimes tinged purplish at the base on the abaxial surfaces, broadly spatulate to obovate, with rounded or ± acute apices, (4.8–)7–8.5 cm. long, 2.5–4.5 cm. wide; stamens numerous, purplish, 7–11 mm. long, the connectives produced into short, apiculate appendages; gynoecia greenish, ca. 2 cm. long at anthesis, thin, spindle-shaped. Fruit aggregates cylindric, often asymmetrical from seed abortion, (4.5–)7–15 cm. long, greenish-pink at dehiscence, becoming brownish, the follicles rounded and discrete prior to dehiscence, lacking stylar beaks; seeds 10–13 mm. long, the outer seed coats red, the inner ones black, ± heart-shaped, with an apiculate apex. $2n = 114$. (*Lassonia heptapeta* Buc'hoz, *M. denudata* Desrouss., *M. conspicua* Salisb., *M. yulan* Desf., *M. precia* Loisel.) — YULAN, LILY-TREE.

Widely cultivated in China and Japan; judged to be native to eastern China in Kiangsu, Anhwei, Chekiang, Kiangsi, and Hunan provinces (see P. J. Savage, Jr., Newsl. Am. Magnolia Soc. 10(2): 3–9. 1974).

The plants referred to by Rehder (1940, p. 251) as *Magnolia denudata* var. *purpurascens* (Maxim.) Rehder & Wilson, Pl. Wilsonianae 1: 401. 1913, excluding the Chinese plant, are apparently not cultivated in North America (*fide* Fogg & McDaniel, 1975), at least under that varietal name. Moreover, the status of these plants is questionable, since Yasui (1937) reported their chromosome number as $2n = 95$, while that of *M. heptapeta* is $2n = 114$. Makino, in treating these plants as a distinct species, *M. purpurascens* (Maxim.) Makino, Jour. Jap. Bot. 6(4): 8. 1929, suggested that they may represent hybrids between *M. heptapeta* and *M. quinquepeta*, in which case the plants would fall under the hybrid group *M.* × *soulangiana* (q.v.).

15. M. sprengeri Pampanini, Nuovo Gior. Bot. Ital. 22: 295. 1915.

FIGURE 4, g–k.

Deciduous trees to 20 m., often of slender pyramidal habit; bark light tannish-gray, smooth and lenticellate, in old plants exfoliating in small flakes; branchlets stout to ± slender, yellowish-green or yellowish-tan, becoming dark purplish-gray and longitudinally fissured, often finely sericeous for 2 or 3 internodes beneath flowers or fruit aggregates of the current or past seasons, otherwise glabrous; terminal winter (mixed) buds finely sericeous to densely woolly with yellowish-white hairs. Petioles 1.5–2.5 cm. long, completely glabrous or occasionally villous at the base of the blades and on the abaxial surfaces opposite the small, adaxial stipule scars; leaf blades 7–13.5(–17) cm. long, 3.8–7(–12) cm. wide, generally less than twice as long as broad, obovate or rarely ovate or broadly elliptic, with cuneate to rounded bases, distally rounded to ±

truncate, the apices abruptly short-acuminate or rarely rounded; upper surfaces of the blades green, glabrous or with scattered hairs appressed along the midveins and major lateral veins, finely reticulate; lower surfaces pale green, reticulate, glabrous or finely appressed-puberulent over the entire surface, or occasionally glabrous except for crisped hairs along the midveins and in the axils of the midveins and major lateral veins. Flowers precocious, fragrant, saucer-shaped, held erect on short glabrous or densely yellowish-sericeous pedicels, the pubescent pedicels soon glabrous; tepals 12(–14), subsimilar, broadly spatulate to oblong-obovate, (4.7–)5.5–12 cm. long, (2.2–)2.5–5.2(–6.5) cm. wide, the abaxial surfaces rosy-red, the adaxial surfaces rosy-red to pale pink; stamens numerous, 10–15 mm. long, rosy-red; gynoecia spindle-shaped, ca. 2 cm. long at anthesis, greenish, the stigmas rosy-red. Fruit aggregates cylindric, often asymmetrical from seed abortion, 6–13 cm. long, the follicles rounded and ± discrete prior to dehiscence, green, becoming dull pink at dehiscence, finally brownish; seeds ca. 1 cm. long, with red outer seed coats, the inner seed coats with a basal pore surrounding a small stalk. $2n = 114$. (*M. denudata* var. *purpurascens* (Maxim.) Rehder & Wilson, excluding synonyms; *M. diva* Stapf ex Millais; including *M. sprengeri diva* Stapf, *M. sprengeri* var. *diva* Stapf ex Johnstone).

Native to Honan, Hupeh, and Szechwan provinces, China.

Small bushy trees, apparently to 15 m. in nature, or large shrubs, $2n = 114$, with the leaves 10.7–14.5 cm. long, 4.1–5.8 cm. wide, oblong-oblanceolate, and usually more than twice as long as broad, and with slightly smaller flowers comprised of white tepals (sometimes tinged with pink) are referable to *Magnolia sprengeri* var. *elongata* (Rehder & Wilson) Johnstone, Asiatic Magnolias Cult. 87. 1955 (*M. denudata* var. *elongata* Rehder & Wilson, *M. sprengeri elongata* (Rehder & Wilson) Stapf), of Hupeh and Szechwan provinces, China.

As is well documented by Stapf (Bot. Mag. **152**: *sub t. 9116.* 1926) and reviewed by Johnstone (1955, pp. 79–89; see also P. J. Savage, Jr., Newsl. Am. Magnolia Soc. **6**(2): 1–5. 1969), there have been considerable nomenclatural and taxonomic difficulties concerning *Magnolia sprengeri* and its subspecific division. Some of this confusion exists because it cannot be determined which of the two customarily recognized varieties of *M. sprengeri* corresponds to the typical variety, var. *sprengeri*. This situation results because the type material of *M. sprengeri*, collected by P. C. Silvestri in northern Hupeh in 1912 and 1913, consists only of flowering specimens, and it is not possible to determine the original color of the dried tepals. Furthermore, since the flowers of *M. sprengeri* are precocious, the specimens lack leaves.

As a result, I am provisionally and arbitrarily designating plants with rosy-red tepals and leaves that are less than twice as long as broad as comprising var. *sprengeri*, while maintaining var. *elongata* for plants with white tepals and leaves generally more than twice as long as broad. This procedure has been adopted previously (see Hilliers' Man. ed. 3, p. 184.

1973), and judging from Wilson's notes (Pl. Wilsonianae 1: 402. 1913) on the relative abundance of the two varieties in nature, it might be expected that Silvestri's collections were from rosy-red-flowered plants. If, however, it were subsequently determined that Silvestri's specimens correspond to var. *elongata*, the correct varietal name for plants with rosy-red flowers would be var. *diva* Stapf ex Johnstone, Asiatic Magnolias Cult. 83. 1955.

The plant figured and discussed by Stapf in the Botanical Magazine under *t. 9116* was one of several plants grown from seed collected in China by Wilson. These plants were initially grown by the Veitch nursery firm in England but were sold in 1913 at the famous Coombe Wood sale to Kew, Caerhays Castle in Cornwall, and Bodnant in northern Wales. Although the entire seed lot (W–688) was ascribed by Wilson to var. *sprengeri* (cited as *M. denudata* var. *purpurascens* (Maxim.) Rehder & Wilson), the plants proved to be variable, and all but one plant at Caerhays (the plant figured in Bot. Mag.) produced white flowers and are referable to var. *elongata*. Apparently, the Caerhays plant represents the only introduction of var. *sprengeri*, and its clonal and seed progeny represent the variety in cultivation in western gardens. As a result of its great horticultural value, the Caerhays plant of *M. sprengeri* var. *sprengeri* and its clonal progeny are usually referred to by the cultivar name 'Diva'. For detailed descriptions of this cultivar, reference should be made to Stapf's article and to that of Johnstone (1955, pp. 83–86, *pl. 9*).

16. **M. sargentiana** Rehder & Wilson, Pl. Wilsonianae 1: 398. 1913.
FIGURE 4, l–o.

Deciduous trees, in nature to ca. 25 m., usually of upright habit, the bark light tannish-gray, warted with conspicuous lenticels, in old plants fissured into irregular platelets; branchlets stout to ± slender, yellowish-green or yellowish-tan, becoming reddish-brown, often with conspicuous whitish lenticels, finely sericeous for 2 or 3 nodes beneath the flowers or fruit aggregates of the current or past seasons, otherwise glabrous; terminal winter (mixed) buds densely woolly with yellowish-white hairs, the vegetative buds finely sericeous to subglabrous. Petioles 1.5–4.5 cm. long, glabrous or with very few scattered hairs, the adaxial surfaces with small basal stipule scars; leaf blades subcoriaceous, (7–)11–18 cm. long, (4.6–)5–10.5(–12) cm. wide, generally less than twice as long as broad, obovate to oblanceolate or broadly elliptic, rarely ± suborbicular, with cuneate, often unequal bases and acute to rounded or sometimes emarginate apices; upper surfaces of the blades light green, ± glossy, reticulate, glabrous; lower surfaces paler green, finely pubescent over the entire surface or on the lamina adjacent to the midveins with ± appressed, curly, silvery or grayish hairs. Flowers fragrant, precocious, ± nodding on short, glabrous to densely sericeous pedicels; tepals subsimilar, 12–14, rarely fewer, 6.4–9 cm. long, 1.4–3.4 cm. wide, spatulate or oblong-

oblanceolate, purplish-pink on the abaxial surfaces, white to pale pink on the adaxial surfaces; stamens numerous, 12–18 mm. long, purplish; gynoecia greenish, with purplish styles, narrowly cylindric, (2–) 2.5–3 cm. long at anthesis. Fruit aggregates cylindric, 9–11 cm. long, often asymmetrical and contorted from seed abortion, reddish-purple at dehiscence, finally dark purplish-brown; follicles ± discrete prior to dehiscence, with obsolete stylar beaks; seeds ca. 1 cm. long, the outer seed coats orangish-red, the inner seed coat with a small basal pore. $2n = 114$. — SARGENT'S MAGNOLIA.

Native to northern Yunnan, Szechwan, and eastern Sikang provinces, China.

Spreading bushy trees usually branched from near the base, with oblanceolate leaves 14.5–20.5(–25) cm. long, 5.9–8.7(–13.5) cm. wide, and more than twice as long as broad, producing larger flowers with (10–)12–16 obovate tepals 8.4–12.5 cm. long and (3.1–)4.5–7.5(–8) cm. wide and larger fruit aggregates 15–19.5 cm. long have been segregated as *Magnolia sargentiana* var. *robusta* Rehder & Wilson, Pl. Wilsonianae 1: 399. 1913. Known only from the type locality (woodlands and open country, Washan) in western Szechwan, var. *robusta*, $2n = 114$, is known to me from E. H. Wilson's type collection and from specimens of cultivated plants apparently grown from his seed collection or their progeny.

The cultivar 'Caerhays Belle' (see F. J. Williams, Jour. Roy. Hort. Soc. 91: 285. *fig. 151.* 1966) represents *Magnolia sargentiana* var. *robusta* × *M. sprengeri* 'Diva', while 'Buzzard' and 'Hawk' are selections from *M. sargentiana* var. *robusta* × *M. campbellii*. Specimens or plants of these hybrids have not been seen.

17. **M. dawsoniana** Rehder & Wilson, Pl. Wilsonianae 1: 397. 1913. FIGURE 4, p.

Deciduous trees to ca. 12 m. or usually large shrubs of ± dense, twiggy growth, the bark ± smooth, tannish-gray, lenticellate; branchlets slender to ± stout, yellowish-green, becoming dark reddish-brown, lenticellate, glabrous or finely sericeous for 1 or 2 internodes beneath the flowers; terminal winter (mixed) buds finely appressed-pubescent with yellowish or silvery hairs. Petioles 1.3–2.9 cm. long, glabrous or finely pubescent within the small, basal stipule scars; leaf blades ± subcoriaceous, 7.5–13.5 cm. long, 5–7.8 cm. wide, broadly elliptic or usually obovate, tapering to cuneate to subrounded, usually unequal bases, the distal ends usually obtuse, rounded, or ± truncate, the apices sometimes abruptly short-acuminate, rarely emarginate; upper surfaces of the blades lustrous dark green, strongly reticulate, finely pubescent along the midveins, sometimes becoming glabrous; lower surfaces paler green, strongly reticulate, glaucous(?), glabrous or with few scattered hairs along the midveins. Flowers fragrant, precocious, held ± horizontally or nodding at the ends of branchlets on stout, glabrous or pubescent pedicels 7–15 mm. long; tepals 9–12, subsimilar, oblong-spatulate to oblanceolate, 7–11(–12.7)

cm. long, 2.1–5(–6.5) cm. wide, white, the abaxial surfaces flushed pale pink; stamens numerous, purplish-red, 12–18 mm. long; gynoecia narrowly cylindric, at anthesis ca. 1.5 cm. long. Fruit aggregates cylindric, 7–10 cm. long, sometimes asymmetrical from seed abortion, reddish-green at dehiscence, becoming dark reddish-brown; follicles rounded and discrete prior to dehiscence, lacking stylar beaks; seeds 7–10 mm. long, the outer seed coats red, the inner black seed coat with a basal pore surrounding a small stalk. $2n = 114$. — DAWSON'S MAGNOLIA.

Known only from the type locality near Tatsien-lu in eastern Sikang Province (formerly in western Szechwan Province), China; very infrequently cultivated in our area.

Closely allied to *Magnolia sargentiana*, *M. dawsoniana* differs from that species in the essentially glabrous under surfaces of its more strongly reticulated leaves, in its flowers with fewer tepals, in its usual shrublike habit, and in the different structure at the base of the inner seed coats.

MAGNOLIA sect. BUERGERIA (Siebold & Zuccarini) Dandy, Camellias and Magnolias, Roy. Hort. Soc. Conf. Rep. 73. 1950.

Deciduous trees and shrubs; flowers precocious; the outer whorl of tepals sepaloid, sometimes caducous, rarely abortive, the inner whorls petaloid. TYPE SPECIES: *M. stellata* Sieb. & Zucc. = *M. kobus* var. *stellata* (Sieb. & Zucc.) Blackburn.

Four species of China and Japan. With the exception of *Magnolia biondii* Pampanini of Shensi, western Honan, western Hupeh, and eastern Szechwan provinces, China, all the species of this section are cultivated in western gardens.

18. **M. cylindrica** E. H. Wilson, Jour. Arnold Arb. 8: 109. 1927.

Small trees to ca. 9 m., with smooth, silvery-gray or tannish bark; young branchlets reddish- or purplish-brown, densely but finely silvery-pubescent, eventually glabrous, emitting a spicy odor when bruised; terminal winter (mixed) buds villous, the hairs yellowish or silvery, the vegetative buds with shorter and fewer hairs. Petioles (9–)12–20(–25) mm. long, finely appressed-pubescent and narrowly grooved along the length of the adaxial surfaces to the basal stipule scars; leaf blades membranaceous to subcoriaceous, (5.7–)8–13.5 cm. long, 1.6–4.8[–6.5] cm. wide, elliptic to oblong-elliptic, [obovate, or oblanceolate], with acute to rounded apices and cuneate to attenuate bases; upper surfaces of the blades glabrous, dark shining green; lower surfaces ± pulverulent to glaucous, finely appressed-puberulent over the surface and along the midveins, occasionally becoming glabrous; in herbarium material the veins of the leaves elevated above the lamina on the upper and particularly the lower surfaces. Flowers [precocious, similar to flowers of *M.*

heptapeta in shape, held erect] on densely silky-pubescent pedicels at the ends of branchlets, [usually subtended by an expanding leaf at anthesis]; tepals [dimorphic, the outer 3 small, membranaceous, sepaloid, 12–15 mm. long, ca. 4 mm. wide], the inner 6 [petaloid, (6.5–)8–10 cm. long, (2.5–)3.5–4(–4.5) cm. wide, broadly spatulate to obovate, white, tinged pink at the base on the adaxial surfaces, the innermost tepals held ± erect until late during anthesis; androecia ca. 13 mm. high, the stamens with broad, flattened, pinkish filaments and acute to rounded apices; gynoecia ca. 1.2 cm. long at anthesis, barely extending beyond the stamens, cylindric-ovoid, greenish]. Fruit aggregates 5–7.5 cm. long, cylindric, 1.8–2.5 cm. in diameter, ± pendent, greenish, tinged purplish or reddish prior to follicle dehiscence, [becoming dark purplish-black on the exterior, the inner follicle walls tan; seeds ca. 1 cm. long, irregularly 2- or 3-faceted]. [$2n = 38$.]

Known with certainty only from the type locality in Anwhei Province, China, where specimens studied by E. H. Wilson were collected by R. C. Ching (*Ching 2949*, A, two sheets!, K!; *2994*, A!, K!) on Wang Shan in 1925. J. E. Dandy, in an annotation on one of these sheets, states that *Ching 2501* from northern Fukien near the Chekiang border is also this species.

Seed, reputedly of *Magnolia cylindrica*, was received in 1936 by the late Mrs. J. Norman Henry of Gladwyne, Pennsylvania, from the Lu Shan Botanic Garden, and plants considered to be *M. cylindrica* now in cultivation in the United States and England are undoubtedly directly or indirectly derived from this original importation. However, the identity and status of the plants now being grown has been questioned, particularly since *M. cylindrica* was based on specimens with immature fruit aggregates, and no flowering material of the species has been examined from China (see J. C. McDaniel, "*Magnolia cylindrica*," the Chinese puzzle, Newsl. Am. Magnolia Soc. 10: 3–7. 1974; N. G. Treseder, *Magnolia cylindrica*, Rhododendrons 1975, with Magnolias and Camellias, Roy. Hort. Soc. 70–72. 1975).

Because of the questionable identity of plants now in cultivation as *Magnolia cylindrica*, the description given here is based on a re-examination of the type material in the herbaria at the Arnold Arboretum and at Kew, while supplemental information based on specimens from the plants in cultivation is included within brackets. A comparison of the protologue and the description presented here (based on the type specimens) will show some discrepancies, particularly concerning the texture of the leaves, a character that has been interpreted to be at variance between the plants in cultivation and the leaves described by Wilson. My comparisons of the type material and specimens of the cultivated plants [4] have satisfied me, however, that the leaves as well as other

[4] The following specimens of *Magnolia cylindrica* from cultivation have been studied (all at AAH): *Witt s.n.*, Univ. Washington Arb., Acc. #741–49, foliage, 3 July 1959; *Krossa s.n.*, Hort. Krossa, Livonia, Michigan, foliage and fruit aggregate,

characters are in agreement. The status of *M. cylindrica* as a distinct species or, as suggested by McDaniel, a putative hybrid involving *M. heptapeta* as one parent cannot be answered until sufficient material, particularly from China, is available for an assessment of variability. The hybridization studies suggested by McDaniel may give interesting results and insights helpful to the determination of the correct taxonomic status of *M. cylindrica*, a taxon that is accepted here provisionally as a species.

19. **M. salicifolia** (Siebold & Zuccarini) Maximowicz, Bull. Acad. Sci. St. Pétersb. 17: 419. 1872. FIGURE 5, o, p.

Large deciduous shrubs or usually small, often slender pyramidal or occasionally widely branching trees to 12 m.; bark warted, dull silvery- or brownish-gray, the young branchlets slender, lenticellate, yellowish-green, becoming dark reddish- or purplish-black, usually emitting a lemony or aniselike odor when bruised; terminal winter (mixed) buds densely villous with long silvery or yellowish hairs, the vegetative buds yellowish or blackish, finely sericeous or with few, short, scattered hairs, occasionally glabrate. Petioles yellowish, (7–)12–20 mm. long, narrowly winged above the basal stipule scars, occasionally puberulent; leaf blades (4–)6.5–12(–16) cm. long, (1.7–)2–5.5(–7) cm. wide, ovate to elliptic or usually lanceolate or oblong-lanceolate, broadest at or below the middle, with acute or rounded apices, irregularly wavy margins, and cuneate, acute, or subrounded, often ± unequal bases; upper surfaces of the blades dull green, glabrous or rarely puberulent, particularly along the midveins; lower surfaces pale green, often ± glaucous, very finely and inconspicuously puberulent over the entire surface or at least adjacent to the elevated, often yellowish midveins. Flowers usually fragrant, precocious, held ± horizontally at the ends of branchlets on glabrous to sparingly villous pedicels, often subtended by an expanding leaf; tepals dimorphic, the outer 3 (rarely more) small, sepaloid, oblong, up to 3.5 cm. long and 1 cm. wide, thin, greenish-white, the inner tepals 6 or occasionally 7 or 8 (rarely to 12), petaloid, white, sometimes greenish or flushed pink at the base on the abaxial surfaces, broadly spatulate, obovate, or oblanceolate in outline, (3.7–)5–9(–12) cm. long, 2–4(–4.5) cm. wide; androecia ca. 1.5 cm. high, the stamens whitish, often pinkish at base, with deltoid to rounded apices; gynoecia 1–1.5 cm. high, green, the styles whitish, slightly recurved. Fruit aggregates cylindric, (3–)4.5–6(–7.5) cm. long, usually symmetrical or occasionally asymmetrical and curved from follicle abortion, at first held ± erect, green, becoming dull pink to reddish as the follicles dehisce, finally dark purplish-black; seeds

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12 Aug. 1965; *Segel & Thompson 211*, Arnold Arb., Acc. #2111–65, plant from Hillier, flowering specimens, 6 May 1975; *Spongberg & Lancaster s.n.*, Hilliers' Jermyns Gardens & Arboretum, foliage and immature fruit aggregates, 10 June 1975. Plants have also been seen at the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania, and the Strybing Arboretum.

FIGURE 5. **Magnolia** sect. **Buergeria.** a–k, *M. kobus* var. *kobus*: a, terminal winter (mixed) bud, × ½; b, habit of flowering branchlet, × ½; c, flower, the inner petaloid tepals removed to show androecium and gynoecium, × 1; d, adaxial view of stamen, × 3; e, transverse section of stamen showing sublateral dehiscence of anther sacs, × 12; f, outline of typical leaf, × ⅓; g, detail of lower surface of leaf blade showing pubescence along major lateral veins and midvein, × 3; h, habit of branchlet with fruit aggregate, × ⅜; i, fruit aggregate with dehisced follicles, × ½; j, seed with outer seed coat intact, × ¾; k, seeds with the outer seed coats removed, × ¾. l, flower of *M. kobus* var. *loebneri* 'Merrill', × ½. m, n, *M. kobus* var. *stellata*: m, flower, × ½; n, outline of typical leaf, × ⅓. o, p, *M. salicifolia*: o, outline of typical leaf, × ⅓; p, detail of lower surface of leaf blade showing puberulence, × 3.

ca. 8 mm. long, the outer seed coats red. $2n = 38$. (*Buergeria salicifolia* Sieb. & Zucc., *Talauma? salicifolia* (Sieb. & Zucc.) Miquel; including *M. salicifolia* var. *fasciata* Millais, *T. salicifolia β concolor* Miquel, *M.* × *proctoriana* Rehder, *M.* × *slavinii* Harkness, and putative hybrids between *M. salicifolia* and *M. kobus* var. *kobus* given the binomial *M.* × *kewensis* S. A. Pearce, an invalid name lacking a Latin description.)
— ANISE MAGNOLIA, WILLOW-LEAF MAGNOLIA.

Endemic to the Japanese islands of Honshu, Shikoku, and Kyushu, where it occurs at moderate elevations in *Fagus* and *Quercus* forests. (See Map 119 in H. Hara & H. Kanai, Distribution maps of flowering plants in Japan. Fasc. 2. Tokyo. 1959.)

Despite the fact that *Magnolia salicifolia* is relatively variable and very closely related to *M. kobus*, it is easily distinguished from that species by the shape and pubescence of its leaves. *Magnolia salicifolia* was originally introduced into western horticulture by C. S. Sargent, but it has been questioned whether the plants grown and distributed by the Arnold Arboretum from Sargent's seed collections were typical *M. salicifolia* (see B. Blackburn, Baileya **5**: 6. 1957; W. J. Bean, 1973, pp. 661, 662). Probably as a result of the skepticism surrounding the original plants and the lack of sufficient knowledge of the variability of *M. salicifolia* in nature, several plants of *M. salicifolia* that appeared as seedlings in cultivation were recognized as hybrids, and numerous plants now in cultivation are currently treated as belonging to hybrid groups. In two of the three instances in which putative hybrids were described, it was postulated that other taxa of sect. BUERGERIA were the pollen parents. Thus Rehder described a hybrid between *M. salicifolia* and *M. kobus* var. *stellata* (pro. sp.), giving the name *M.* × *proctoriana* to the hybrid group (Jour. Arnold Arb. 20: 412. 1939), while S. A. Pearce (Gard. Chron. III. 132: 154. 1952) gave the collective name *M.* × *kewensis*[5] to presumed hybrids between *M. salicifolia* and *M. kobus* var. *kobus*. A third hybrid originally assumed to involve *M. salicifolia* as the seed parent and *M.* × *soulangiana* as the pollen parent was named *M.* × *slavinii* Harkness (Natl. Hort. Mag. 33: 118. 1954). However, this hybrid was later (Morris Arb. Bull. 12: 19. 1961) reduced to the synonymy of *M.* × *proctoriana*, since its chromosome number, $2n = 38$, did not coincide with the number to be expected had *M.* × *soulangiana*, $2n = 95, 114$, been the pollen parent.

However, a re-examination of the morphology of the three presumed hybrids (including the type specimens of *Magnolia* × *proctoriana* and

[5] The original plant of this putative hybrid and its clonal progeny are now generally known under the cultivar name 'Kewensis'. An alternative designation utilizes the formula *M. salicifolia* × *M. kobus* to cover all progeny of this cross, but if Blackburn's taxonomy (1955, 1957) is adopted concerning *M. kobus* and its varieties, as it is here, the name *M.* × *proctoriana*, as a collective epithet, covers all hybrids between *M. salicifolia* and *M. kobus*. For reasons discussed above, however, these hybrids are repudiated and the name *M.* × *proctoriana* is placed in the synonymy of *M. salicifolia*.

specimens from the "type" plants of *M.* × *slavinii* and *M.* × *kewensis*) and that of the assumed parental taxa has convinced me that the "hybrids" are easily accommodated within *M. salicifolia*. This conclusion is supported when the variation of *M. salicifolia* in nature is studied in conjunction with the cultivated material. The fact that seedlings of *M. salicifolia* show a degree of variability is undoubtedly correlated to some extent with the fact that the species is self-compatible (see J. C. McDaniel, Newsl. Am. Magnolia Soc. 2: 4. 1965), and plants grown from self-fertilized seeds should be expected to exhibit variation associated with the expression of recessive traits. Support for the nonhybrid status of these plants also comes from the cytological condition found in plants grown as *M.* × *proctoriana*. F. S. Santamour, Jr. (Morris Arb. Bull. 21: 80. 1970) found that at meiosis "pairing at metaphase I was regular, with 19 bivalents being formed. Pollen abortion was only 7% and the grains averaged 36.9 μ in diameter."

Among the cultivars of *Magnolia salicifolia*, 'Slavin's Snowy' (see B. Harkness, Morris Arb. Bull. 12: 19. 1961) and 'Wada's Memory' (see B. Mulligan, Arb. Bull. 22: 20, 21. 1959) are of particular merit because of their abundant large flowers.

20. **M. kobus** De Candolle, Reg. Veg. Syst. Nat. 1: 456. 1817.

FIGURE 5, a–n.

Deciduous shrubs or usually trees to 20 m., the trees occasionally with a single bole, often with several limbs from near the base and widely branching; bark warted, dull to clear silvery or brownish-gray, becoming ± ridged on old trunks; young branchlets slender to ± stout, glabrous or occasionally finely sericeous, lenticellate, yellowish-green, becoming dark reddish or purplish-black, usually emitting a turpentinelike odor when bruised; terminal winter (mixed) buds densely villous with long silvery or yellowish-brown hairs, the vegetative buds usually blackish, occasionally yellowish or greenish, finely to densely sericeous. Petioles yellowish-green, (0.1–)1–2.5(–3) cm. long, narrowly winged or shallowly grooved along the length of the adaxial surfaces above the basal stipule scars; leaf blades (3.2–)4.5–14.5(–16.5) cm. long, (2.5–)4–8.3 (–9.5) cm. wide, rarely elliptic, usually obovate to oblanceolate, widest at or above the middle, with acute, abruptly short-acuminate, or occasionally rounded apices, ± wavy, often undulate margins, and attenuate to cuneate, often oblique, bases; upper surfaces of the blades dark green, glabrous; lower surfaces pale green, glabrous or with long hairs scattered along the elevated veins and in the axils of the midveins and major lateral veins. Flowers precocious, usually ± fragrant, held ± horizontally at the ends of branchlets on finely to densely pubescent pedicels, usually subtended by an expanding leaf at anthesis; tepals dimorphic, the outer 3 (rarely more) small, sepaloid, persistent at anthesis, oblong, (0.6–)1.5–3.5(–4) cm. long, (0.2–)0.3–0.5(–1) cm. wide, usually greenish- or brownish-white, rarely pure white, the inner tepals usually 6, sometimes 5 or 7, petaloid, white, usually suffused with pink at the base on

the abaxial surface, (5–)6–7(–9.8) cm. long, (1.3–)2–3.5(–4.2) cm. wide, narrowly to broadly spatulate to oblanceolate or sometimes obovate in outline; androecia ca. 1.5 cm. long, the stamens usually pinkish or purplish at base; gynoecia 1–1.5 cm. long at anthesis, cylindric, green, the styles whitish. Fruit aggregates held ± horizontally, cylindric and symmetrical or often curved, asymmetrical and constricted between some follicles owing to seed abortion, 3.5–11 cm. long, green at first, becoming pinkish or reddish at dehiscence, warted with whitish outgrowths, finally reddish-brown; seeds ca. 9 mm. long, usually slightly wider, with red outer seed coats. $2n = 38$. (*M. thurberi* Parsons; *M. praecocissima* Koidzumi; including *M. kobus* var. *borealis* Sarg.) — KOBUS MAGNOLIA.

Relatively common at moderate elevations throughout Japan; also known from Quelpaert Island, South Korea.

As is well outlined by Johnstone (1955, pp. 92–94), the rationale for the inclusion of var. *borealis* Sarg., Trees & Shrubs 2: 57. 1908, within var. *kobus* is based on the fact that there are no clear-cut distinguishing characters that separate the northern plants from the southern ones.

Aside from *Magnolia kobus* var. *kobus*, above, two additional, horticulturally important varieties of *M. kobus* are recognized here; the status accepted for var. *stellata* follows the treatment proposed by Blackburn (Baileya **5**: 3–13. 1957).

Magnolia kobus var. *stellata* (Sieb. & Zucc.) Blackburn, Amatores Herbarii 17: 1. 1955 (*Buergeria stellata* Sieb. & Zucc.; *Magnolia stellata* (Sieb. & Zucc.) Maxim.; *M. halleana* Parsons; *M. kobus* f. *stellata* (Sieb. & Zucc.) Blackburn; including *M. stellata* var. *rosea* Veitch, *M. stellata* var. *keiskei* Makino), $2n = 38$, Star magnolia, is distinguished from var. *kobus* by its habit as a low, twiggy shrub or small tree with finely sericeous young branchlets, its narrower, elliptic or usually obovate to oblanceolate leaf blades (1.8–)6–13.2 cm. long and (0.8–)2.5–6.5 cm. wide, with rounded, obtuse, acute, or abruptly short-acuminate apices, and its flowers with numerous (12–33), narrowly oblong, petaloid tepals 0.6–1.4(–1.7) cm. wide and 4–6.5 cm. long, sometimes suffused with pink on the abaxial surfaces. The outermost whorl of three small sepaloid tepals in flowers of var. *stellata* is often caducous, falling with the stipular bud scales as the flowers expand, or sometimes it is abortive. A Japanese plant, var. *stellata* has a reputedly natural area of distribution in the mountains of the western Tōkaidō District of southern Honshu. It has been questioned, however, whether this taxon actually occurs or did occur in the spontaneous flora of Japan or whether it was of garden origin (see N. G. Treseder, Newsl. Am. Magnolia Soc. **8**(2): 8. 1972). The question is perhaps justified, since var. *stellata* is widely grown in Japan as an ornamental, and the few records of its occurrence as a wild plant are questionably valid.

Among the cultivars of *Magnolia kobus* var. *stellata*, several are of particular horticultural interest. These include 'Royal Star', a very hardy upright small tree that blooms later in spring than most plants of var. *stellata*, with the flowers, as a result, less subject to frost damage; 'Rosea'

(= *M. stellata* var. *rosea* Veitch, Jour. Hort. Soc. London 27: 865. *fig. 196.* 1902), with the tepals suffused with reddish pink on the abaxial surfaces in bud, fading to near white during anthesis; 'Centennial' (see Avant Gard. 5(24): 1. 1973), with larger and more numerous pure white tepals than are found in most clones; and 'Waterlily', another clone of vigorous and fast-growing plants with water-lilylike flowers, pinkish in bud.

An F_1 generation of sterile, triploid hybrids, $2n = 57$, between *Magnolia kobus* var. *stellata* and *M. quinquepeta* (as *M. liliflora*) that are multiple–stemmed, rounded or conical shrubs with erect terminal winter (mixed) buds, glabrous branchlets, *quinquepeta*-like leaves, and *stellata*-like flowers has been produced at the United States National Arboretum, and eight named cultivars selected from these hybrids have been distributed to several arboreta and commercial nurseries. The cultivars, 'Ann', 'Betty', 'Jane', 'Judy', 'Pinkie', 'Randy', 'Ricki', and 'Susan', are fully described by T. R. Dudley and W. F. Kosar (Morris Arb. Bull. 19: 26–29. 1968; *Ibid.* 20: 64, 65. 1969).

Intraspecific hybrids between *Magnolia kobus* var. *kobus* and *M. kobus* var. *stellata* have resulted from deliberate and chance crosses, and owing to the desirability of a name for these horticulturally important plants, the hybrid group is recognized here as **M. kobus** var. **loebneri** (Kache) Spongberg, comb. et stat. nov. (Basionym: *Magnolia* × *loebneri* Kache, Gartenschönh. 1: 20. 1920). Plants of var. *loebneri* are generally small trees and occasionally shrubs with young branchlets sparingly sericeous; variable leaf blades narrowly oblanceolate to obovate, broadly elliptic or oblong, 6.5–14.3 cm. long, 2.3–6.1 cm. wide, the apices obtuse, rounded, or abruptly short-acuminate, rarely ± retuse; and flowers held ± horizontally and comprised of 3 outer, sepaloid tepals and 11–16 narrowly to broadly spatulate petaloid tepals (1.3–)1.6–3 cm. wide and 5–7.9 cm. long, the abaxial surfaces sometimes flushed pink. This hybrid group was first recognized as the result of deliberate crosses made between var. *kobus* and var. *stellata* by Max Löbner of Pillnitz, Germany, shortly before World War I. Additional intentional crosses have been made, while chance crosses in cultivation have been recognized, and several of the exceptional progeny have received cultivar names. The most outstanding cultivars include 'Merrill' (see D. Wyman, Arnoldia 12: 45. *pl. 12.* 1952), 'Spring Snow', and 'Ballerina' (for both see J. C. McDaniel, Newsl. Am. Magnolia Soc. 7(1): 1–3. 1970), all with large, exceptionally showy white flowers, and 'Leonard Messel' (see Jour. Roy. Hort. Soc. 94: 522. 1969; Newsl. Am. Magnolia Soc. 9(1): 6, 7. 1973), with lilac-pink flowers.

Magnolia sect. Tulipastrum (Spach) Dandy, Camellias and Magnolias, Roy. Hort. Soc. Conf. Rep. 74. 1950.

Deciduous trees and shrubs; flowers occasionally precocious (but then continuing with the leaves), usually appearing with the leaves; outer

whorl of tepals sepaloid, sometimes caducous, the inner petaloid tepals greenish to yellow or purple. TYPE SPECIES: *M. acuminata* L.

Two species, one of eastern North America and the second widely cultivated since ancient times in China and Japan, judged to be native to China.

21. **M. quinquepeta** (Buc'hoz) Dandy, Jour. Bot. 72: 103. 1934.

Deciduous shrubs with grayish bark, to ca. 3 m., occasionally larger, spreading or upright, usually ± straggly in habit, sometimes suckering from the roots; branchlets green, becoming purplish-brown, glabrous, sparingly lenticellate; terminal winter (mixed) buds finely but densely sericeous with yellowish or silvery hairs, becoming narrow and ± sickle-shaped when expanding, the vegetative buds finely sericeous. Petioles 1–2 cm. long, finely sericeous, with elongate, pubescent stipule scars extending almost to the base of the leaf blades; leaf blades broadly elliptic to oblong-obovate or oblanceolate, (10–)13–20 cm. long, (4.5–)6.5–10 (–11.5) cm. wide, tapering ± gradually to acute to rounded, rarely abruptly short-acuminate apices and cuneate to attenuate bases, the lamina usually decurrent along the petiole to the stipule scar; upper surfaces of the blades dark green, finely pubescent along the midveins, otherwise glabrous or with few, scattered hairs over the lamina; lower surfaces pale green, glabrous or sometimes with hairs along the midveins, rarely with hairs over the lamina. Flowers sometimes precocious, but continuing after the leaves have expanded, often with a second period of bloom in fall, ± vase-shaped, odorless or faintly fragrant, held ± erect on stout, sericeous pedicels; tepals dimorphic, the outer whorl of 3 or 4 sepaloid, 2–3.5 cm. long, 5–7(–10) mm. wide, greenish or purplish, caducous, the inner tepals 6(–10), petaloid, narrowly lanceolate to spatulate, (6.5–)8–10(–13) cm. long, (2–)3–4.5(–5.1) cm. wide, the abaxial surfaces purplish, the adaxial surfaces whitish to light purple; stamens 8–10 mm. long, purplish, the connectives produced into short, acute appendages; gynoecia ca. 1.5 cm. long at anthesis, the carpels purplish. Fruit aggregates apparently rarely formed, those examined cylindric to subglobose, 3.5–5.5 cm. long, dark purplish-brown; follicles rounded prior to dehiscence, with short stylar beaks; seeds ca. 1 cm. long. $2n = 76$. (*Lawsonia quinquepeta* Buc'hoz; *M. liliflora* Desrouss. in Lamarck; *M. obovata* Thunberg, quoad syn.; *M. discolor* Ventenat; *M. purpurea* Curtis; *M. denudata* Schneider, not Desrouss.)

Cultivated in China and Japan since ancient times but judged to be native to China, "probably of the warm temperate districts south of the Yangtsze river" (Rehder & Wilson, Pl. Wilsonianae 1: 403. 1913).

Several cultivars of *Magnolia quinquepeta* have been named (see J. C. McDaniel, Newsl. Am. Magnolia Soc. 9(2): 20–23. 1973; Fogg & McDaniel, 1975), and the following two were accounted for by Rehder

(1940, 1949): 'Nigra' (= *M. liliflora* var. *nigra* (Nicholson) Rehder in Bailey, Std. Cycl. Hort. **4**: 1968. 1916; *M.* × *soulangiana nigra* Nicholson, Gard. **25**: *276, 277. pl. 434*, 1884), a plant with large flowers, the petaloid tepals ca. 12 cm. long, intensely dark purple abaxially, light purple within; 'Gracilis' (= *M. liliflora* var. *gracilis* (Salisbury) Rehder in Bailey, Std. Cycl. Hort. **4**: 1968. 1916; *M. gracilis* Salisbury, Parad. Londin. 2: *t. 87*. 1807), a small shrub with narrow leaves and small, dark purple flowers. It would appear that these cultivar names have been used for several similar clones, and it is probably impossible to distinguish the direct clonal progeny of the plants to which these names were originally applied.

Magnolia quinquepeta is the pollen parent of the hybrid group *M.* × *soulangiana* (q.v.), while triploid hybrids between *M. kobus* var. *stellata* and *M. quinquepeta*, $2n = 57$, have been produced at the United States National Arboretum and are discussed briefly under *M. kobus*. *Magnolia quinquepeta* 'Nigra' (as *M. liliflora* var. *nigra*) is also the pollen parent of *M.* × *brooklynensis* Kalmbacher (Newsl. Am. Magnolia Soc. **8**(2): 7, 8. 1972; *Ibid.* 9(1): 12, 13. 1973), $2n = 78$, a hybrid group involving *M. acuminata* as the seed parent. The type clone of this hybrid group is 'Evamaria', while J. C. McDaniel has introduced another cultivar, 'Woodsman' (see Newsl. Am. Magnolia Soc. **9**(1): 13, 14. 1973; *Ibid.* **10**(2): 23. 1974; Am. Horticulturist **54**(1): 10–13. 1975). *Magnolia* × *brooklynensis*, as well as *M. quinquepeta* × *M. sprengeri*, *M. quinquepeta* × *M. campbellii*, and the trihybrids between *M. quinquepeta* and *M.* × *veitchii* (see D. T. Gresham, Morris Arb. Bull. 13: 47–50. 1962), is not described here, since documenting herbarium specimens and/or living plants have not been seen.

22. M. acuminata (Linnaeus) Linnaeus, Syst. Nat. ed. 10. 2: 1082. 1759.

Large deciduous trees usually of pyramidal form, to 30 m., the brownish-gray bark furrowed into ridges; branchlets reddish-brown, becoming silvery-tan, lenticellate, sometimes pubescent at the nodes, otherwise glabrous; terminal winter (mixed) buds finely sericeous with closely appressed, silvery hairs. Petioles (1.5–)2.5–3.5(–5) cm. long, with basal stipule scars, silvery-sericeous, sometimes becoming subglabrous; leaf blades ± membranaceous, elliptic to broadly ovate, oblong-ovate, or occasionally oblong-obovate, 10–24 cm. long, with acute to abruptly acuminate or sometimes obtuse apices and rounded or truncate to acute or cuneate, often unequal bases; upper surfaces of the blades dark green, sparingly puberulent over the surface, becoming glabrous; lower surfaces paler green, ± glaucous, finely puberulous to densely sericeous, particularly adjacent to the veins, sometimes becoming subglabrous. Flowers appearing with the leaves, ± cup-shaped, held ± erect on glabrous or occasionally densely villous pedicels 1.5–3 cm. long; tepals 9, greenish to greenish-yellow throughout, sometimes purplish-tinged, glau-

cous, the outer whorl of 3 smaller than the inner 6, sepaloid, ca. 2 cm. long, becoming reflexed, the inner tepals petaloid, 3–9(–10) cm. long, 1–3 cm. wide, oblanceolate to oblong-spatulate; stamens numerous, ca. 1 cm. long, the filaments well defined; gynoecia ca. 2.5 cm. long at anthesis. Fruit aggregates ± ovoid to oblong-cylindric, often asymmetrical from seed abortion, (3–)3.5–5(–7) cm. long, green, becoming pinkish at dehiscence, finally dark reddish-brown; follicles rounded, lacking stylar beaks; seeds 9–11 mm. long, the outer seed coats reddish-orange. $2n = 76$. (*M. virginiana* ϵ *acuminata* L.; *Tulipastrum acuminatum* (L.) Small; including *M. acuminata* var. *ludoviciana* Sarg., *M. acuminata* var. *ozarkensis* Ashe.) — CUCUMBER-TREE.

A variable species widely distributed in eastern North America from southern Ontario and New York southward to Alabama, Mississippi, and Louisiana, and west to Arkansas and eastern Oklahoma. (See E. L. Little, Jr., Atlas of U. S. Trees 1: *map 140-E.* 1971; J. C. McDaniel, Newsl. Am. Magnolia Soc. 9(2): 9–14. 1973; *Ibid.* 10(2): 21, 22. 1974.)

Plants with the outer petaloid tepals greenish-yellow and the inner petaloid tepals clear golden yellow have been recognized as *Magnolia acuminata* f. *aurea* (Ashe) Hardin, Jour. Elisha Mitchell Sci. Soc. 70: 306. 1954 (*Tulipastrum acuminatum* var. *aureum* Ashe). This yellow-flowered form of *M. acuminata* occurs sporadically in the mountains and upper Piedmont of the Carolinas, Georgia, and Tennessee, while plants comprising *M. acuminata* var. *subcordata* (Spach) Dandy, Am. Jour. Bot. 51: 1056. 1964 (*Tulipastrum americanum* var. *subcordatum* Spach; *M. cordata* Michx.; *M. acuminata* var. *cordata* (Michx.) Sarg.; including *M. acuminata* var. *alabamensis* Ashe), also commonly with yellow flowers, are native to the Piedmont and Coastal Plain from central North Carolina to central Alabama. Usually trees or sometimes large shrubs, plants of var. *subcordata* are distinguished from plants of var. *acuminata*, described above, by the young branchlets densely sericeous with close, silvery hairs or at least roughened by the bases of these hairs, the lower surfaces of the leaf blades closely tomentose, and the yellow or sometimes greenish-yellow flowers borne on densely villous, rarely glabrous, pedicels. As noted by Hardin (1954), intermediates between the two varieties occur, and reference should be made to Hardin's paper for a more detailed and complete comparison of the two taxa.

The hardiest of the America species of *Magnolia*, *M. acuminata* is often used as rootstock for grafting other, more tender species. *Magnolia acuminata* is also the seed parent of hybrids with *M. quinquepeta*, known under the collective epithet *M.* × *brooklynensis*; these are discussed briefly under *M. quinquepeta*.

HYBRIDS

23. M. virginiana Linnaeus × M. grandiflora Linnaeus.

Evergreen or sometimes deciduous trees to 10 m. (perhaps more), of spreading or erect, columnar habit; branchlets stout, with septate pith, at first thickly to thinly felted with rufous or yellowish hairs, the older growth eventually glabrous, green or yellowish-green, becoming reddish-brown; buds densely sericeous with rufous or silvery-rufous hairs. Petioles stout, (1–)1.5–2(–2.5) cm. long, densely sericeous with rufous hairs, the density often decreasing with age, with small, often obscured, pubescent, basal stipule scars on the adaxial surfaces; leaf blades stiffly coriaceous, 8.8–18(–22) cm. long, 4–8.5(–10) cm. wide, elliptic, oblong-lanceolate, ± oblong-ovate to broadly ovate, with attenuate bases, entire ± undulate margins, tapering slightly to rounded or rarely retuse apices; upper surfaces of the blades dark, glossy green, at first with hairs scattered over the lamina and on the midveins, the hairs along the midveins often persistent, the lamina, when dried, finely reticulated in a ± honeycomb pattern; lower surfaces ± glaucous, often densely felted with rufous or silvery-rufous hairs, often less densely so in age. Flowers cup-shaped, lemony-fragrant, occurring intermittently throughout the growing season, borne erect on densely silvery-, yellowish-, or rufous-felted pedicels 1–2 cm. long; tepals 9–12(?), white, broadly spatulate to subglobose in outline, 5.5–9 cm. long, 2.7–5.5 cm. wide; stamens ca. 12 mm. long, numerous, rosy-purple; gynoecia ca. 2 cm. long at anthesis, carpels finely pubescent, the styles glabrous. Fruit aggregates rarely developed, when formed often asymmetrical, ± subglobose, ca. 4 cm. long, the follicles finely sericeous; seeds not seen. $2n = 76$.

As noted by O. M. Freeman (Natl. Hort. Mag. **16**: 161, 162. 1937) when he first described this hybrid group, which resulted from cross-pollinations made by him in 1930 and 1931, plants of this parentage resemble *Magnolia grandiflora*, the pollen parent, more closely than *M. virginiana*, the seed parent. Two cultivars have been selected from these hybrids and represent the group in cultivation. 'Freeman' (see U. S. D. A. plant inventory no. 169, P. I. 277263; F. G. Meyer, Newsl. Am. Magnolia Soc. **8**(1): 7, 8. 1971), a selection from the F_1 generation, is a plant of narrow columnar habit propagated fairly easily from vegetative cuttings of half-ripened wood. 'Maryland' (see F. G. Meyer, Newsl. Am. Magnolia Soc. **8**(1): 8, 9. 1971), another selection from the F_1 generation, is a plant of spreading habit that was also named because of the relative ease with which its vegetative cuttings can be rooted.

Apparently the cultivar 'Griffin' (Fogg & McDaniel, 1975, p. 16) represents a spontaneous hybrid between *Magnolia virginiana* and *M. grandiflora*.

24. M. × wieseneri Carrière, Rev. Hort. 62: 406. 1890. [*Magnolia hypoleuca* × *M. sieboldii*.]

Small, deciduous, bushy trees or large shrubs to ca. 7 m., usually with long branchlets and of rather ungainly habit; branchlets ± stout, at first sparingly appressed-pubescent with silvery hairs, soon glabrous, green, becoming yellowish- or reddish-brown, the periderm exfoliating in thin sheets; terminal winter (mixed) buds ± glaucous, sparingly pubescent. Leaves alternate, the internodes at the ends of branchlets often short and the leaves in somewhat loose, false whorls; petioles slender to stout, (1.7–)2.4–3(–5.5) cm. long, subglabrous to finely sericeous with silvery hairs, the adaxial surfaces with prominent stipule scars; leaf blades (9.8–)13.8–19(–22) cm. long, (5–)7.4–10.5(–12.3) cm. wide, broadly elliptic to obovate, tapering to cuneate to acute, sometimes unequal bases and acute to rounded apices, the margins entire, often undulate; upper surfaces of the blades green, often with scattered hairs along the midveins and the 10–15 pairs of major lateral veins, otherwise glabrous; lower surfaces glaucous, finely sericeous along the elevated midveins and sparsely appressed-pubescent over the entire surface with ± straight or crisped hairs, usually with reddish pigment in the crosswalls. Flowers fragrant, ± cup-shaped, held erect on stout, glabrous or puberulent pedicels 3–8 cm. long; tepals 9, the outer whorl of 3 white tepals becoming ± reflexed and flushed pink in age, the inner 6 tepals creamy white, broadly obovate, with rounded apices and narrowed bases, 5.5–6 cm. long, 2–3.5 cm. wide; stamens numerous, rosy-crimson, 1.5–2 cm. long, the apices rounded, blunt, or occasionally apiculate; gynoecia ca. 3 cm. long at anthesis. Fruit aggregates and seeds not seen. $2n = 38$. (*Magnolia* × *watsonii* J. D. Hooker.)

A putative hybrid between *Magnolia hypoleuca* and *M. sieboldii*, apparently of garden origin in Japan. First introduced into western horticulture by the Japanese at the 1889 International Exposition in Paris, plants of this parentage have generally been known as *M.* × *watsonii* J. D. Hooker. However, Carrière's name for this hybrid group was published on 1 September 1890, while Hooker's description (Bot. Mag. 117: *sub. t. 7157*) is dated 1 February 1891, thus necessitating under the rule of priority the adoption of Carrière's name for all hybrids of this parentage.

The description given here has been based on five specimens, two of Japanese origin, including a 1918 Wilson collection from the grounds of the Yokohama Nursery Company, Ltd. While most closely resembling *Magnolia sieboldii*, *M.* × *wieseneri* can be readily distinguished from that species by several characters, including the greater number of major lateral veins in the leaf blades, the erect position of the flowers, the longer stamens, and the larger gynoecium. From *M. hypoleuca* the hybrids differ in habit, in the smaller leaves with fewer lateral veins, in the pubescent young branchlets, and in the smaller tepals.

25. **M. × thompsoniana** (Loudon) C. de Vos, Nederl. Fl. & Pomon. 131. *t. 43*. 1876. [*Magnolia virginiana* × *M. tripetala*.]

Usually deciduous or occasionally semievergreen shrubs or small trees to ca. 8 m., sometimes of loose, ungainly habit, reminiscent of *Magnolia virginiana*; branchlets yellowish-green, becoming reddish-brown, lenticellate; pith incompletely septate; terminal winter (mixed) buds greenish or yellowish-brown, glaucous. Leaves alternate, the internodes at the ends of branchlets often short and the leaves sometimes appearing to be in false whorls; petioles yellowish-green, (1.4–)1.8–2.5(–3.5) cm. long, finely puberulent along the length of the adaxial surface above the basal stipule scar; leaf blades elliptic or occasionally oblanceolate, (5.5–)12–17.5(–22) cm. long, (2.4–)5.5–7.5(–8.5) cm. wide, with entire, ± undulate margins, cuneate bases, and acute apices; upper surfaces of the blades green, shining, often with short hairs scattered along the midveins, otherwise glabrous; lower surfaces silvery- or grayish-green, glaucous, finely appressed-puberulous with silvery hairs over the entire surface, particularly along the elevated midveins. Flowers ± vase-shaped, pleasantly fragrant, held erect at the ends of branchlets on relatively stout, glaucous pedicels (1.5–)2.4–3.5 cm. long; tepals 9, the outer 3 greenish-white, spatulate in outline, with relatively broad bases, becoming ± reflexed, the inner 6 tepals creamy white, oblong-obovate, 7–9 cm. long, 2.4–3.5(–4) cm. wide, with rounded apices and narrowed, ± clawed bases; stamens 1–1.5 cm. long, the connectives produced into short, acute appendages; gynoecia greenish, ca. 2 cm. long at anthesis. Fruit aggregates 4–5 cm. long, cylindric, green, becoming pinkish; seeds not seen. $2n$ = 38. (*M. glauca* var. *major* Sims; *M. glauca* var. *thompsoniana* Loudon.) — THOMPSON'S MAGNOLIA.

A chance hybrid between *Magnolia virginiana* and *M. tripetala* first described in 1820 (Bot. Mag. 47: *t. 2164*) from a plant grown from seed in the nursery of Archibald Thompson at Mile End, London, England. Plants of this parentage known to me in cultivation are in most characters intermediate between the two parental species. In habit they are perhaps most easily confounded with *M. virginiana*. However, the incompletely septate pith of branchlets of *M.* × *thompsoniana* contrasts with the distinctly and completely septate pith of *M. virginiana*; this character should aid in identification at any season of the year. This hybrid has recently been recreated as a result of intentional cross-pollinations of the parent species (see J. C. McDaniel, Illinois Research, Ill. Agr. Expt. Sta., pp. 8, 9. Fall, 1966), and the sterility of the hybrids has also been investigated (see F. S. Santamour, Jr., Morris Arb. Bull. 17: 29, 30. 1966).

Specimens that I have seen of hybrids between *Magnolia virginiana* and *M. hypoleuca*, mentioned under the latter species, are almost indistinguishable from specimens of *M.* × *thompsoniana*.

26. M. × veitchii auct. ex Gard. Chron. III. 69: 154. *fig. 68.* 1921; emend. J. W. Bean in Veitch, Jour. Roy. Hort. Soc. 46: 321. 1921. [*M. heptapeta* × *M. campbellii.*]

Vigorous deciduous trees to 30 m., when in flower similar in appearance to *M.* × *soulangiana*; bark ± smooth, lenticellate, silvery-tan, the branchlets glabrous or with few, scattered hairs, ± stout, dark purplish-brown, lenticellate. Petioles finely pubescent, 2.5–3 cm. long; leaf blades obovate to oblong, (11.5–)14.3–22 cm. long, (6.5–)8.6–11.6 cm. wide, abruptly short-acuminate or acute at the apices, the bases cuneate to ± rounded, unequal; upper surfaces of the blades dark green, with short hairs along the veins, otherwise glabrous; lower surfaces reticulate, finely sericeous along the mid and lateral veins, sometimes on the lamina as well. Flowers precocious, ± vase-shaped, held erect on stout, finely pubescent pedicels 1–1.4 cm. long; tepals 7–10, subequal, white flushed pink to purple on the abaxial surfaces, the adaxial surfaces very pale pink or whitish, or the tepals white on both surfaces, obovate to broadly spatulate, narrowed basally into a claw, (6.3–)9–12.2 cm. long, (2.5–)4.5–5.9 cm. wide, the inner tepals held ± erect, partially enclosing the androecium and gynoecium; stamens (1.3–)1.5–2.2 cm. long, purplish; gynoecia 1.8–2.3 cm. long at anthesis. Fruit aggregates 7–10 cm. long, cylindric, usually contorted and asymmetrical from seed abortion, pinkish-green at dehiscence, becoming dark purplish-brown; seeds with red outer seed coats, ca. 7 mm. long. $2n = 114(?)$. — VEITCH'S MAGNOLIA.

The name *Magnolia* × *veitchii* is applied to hybrids between *M. heptapeta* and *M. campbellii*. These hybrids were first obtained by P. C. M. Veitch in England in 1907. Of five plants grown from the original hybrid seed, one plant produced flowers with pinkish tepals, while the remaining four plants produced white flowers. The pink-flowered plant, the form most often encountered in cultivation, is known by the cultivar name 'Peter Veitch'.

27. M. × soulangiana Soulange-Bodin, Mém. Soc. Linn. Paris 1826: 269. 1826; Ann. Soc. Hort. Paris 1: 90. 1827. [*M. heptapeta* × *M. quinquepeta.*]

Deciduous trees or sometimes large shrubs, usually of densely twiggy habit; bark silvery-gray, ± smooth, with prominent horizontal lenticels; branchlets purplish-brown, ± stout, glabrous or at first finely appressed-pubescent; terminal winter (mixed) buds grayish, finely sericeous with yellowish or silvery hairs, the vegetative buds silvery-pubescent. Petioles 0.7–3 cm. long, stout, finely sericeous, with short, basal stipule scars on the adaxial surfaces; leaf blades membranaceous to ± subcoriaceous, broadly elliptic to oblong-oblanceolate or broadly obovate to suborbicular, usually abruptly short-acuminate (the apex itself rounded) or sometimes ± rounded, and tapering to cuneate to subrounded, often unequal bases, (5.5–)7.5–16.2(–22) cm. long, (2.8–)3.1–11.5(–12.5) cm. wide; upper

surfaces of the blades reticulate, dark, ± glossy green, with short, crisped hairs along the midveins and major lateral veins, sometimes with scattered hairs on the lamina as well; lower surfaces reticulate, paler green, with sericeous pubescence along the veins and not uncommonly puberulent over the lamina. Flowers precocious, often continuing until after the leaves have expanded, variable in size, shape, and coloring, generally goblet-, cup-, or saucer-shaped, fragrant or odorless, held ± erect on stout, densely sericeous pedicels 5–7 mm. long; tepals 9, white or white flushed or variously streaked pink to dark purple on the abaxial surfaces, the adaxial surfaces white to pinkish, subsimilar, the outer whorl sometimes ca. half the length of the inner tepals, 6–11(–15) cm. long, 2.7–7(–9) cm. wide, generally spatulate to obovate or oblanceolate, or rarely the outer whorl greenish and sepaloid, when present, ca. 4 cm. long, 1.2 cm. wide; stamens numerous, usually pinkish to purplish, 8–12(–15) mm. long; gynoecia 1.5–2 cm. long at anthesis. Fruit aggregates cylindric, 5–10(–11.5) cm. long, often contorted and asymmetrical from seed abortion, pinkish-green at dehiscence, finally dark reddish-purple; follicles rounded, lacking stylar beaks; seeds ca. 12 mm. long, the outer seed coats red. $2n = 95, 114(?)$. (*M. speciosa* Van Geel; *M. conspicua* var. *soulangiana* Hort. ex Pampanini.) — SAUCER MAGNOLIA.

Perhaps the most widely cultivated *Magnolia* in western gardens, *M.* × *soulangiana* comprises a variable group of hybrids between *M. heptapeta* and *M. quinquepeta*, which were first grown by C. E. Soulange-Bodin of Fromont, France, in 1820, apparently as the result of deliberate cross-pollinations. Although partially sterile, a multitude of forms of *M.* × *soulangiana* have appeared in cultivation since that time, and it would appear that owing to segregation in the F_2 and succeeding generations and, perhaps, introgression, several forms approach or merge with *M. heptapeta*, the original seed parent, and *M. quinquepeta*. As a result, identification of particular plants is difficult, if not impossible, without knowledge of chromosome number, and a thorough investigation of *M.* × *soulangiana*, particularly in relation to *M. heptapeta*, is needed. Generally, plants of *M.* × *soulangiana* can be distinguished from *M. heptapeta* by their later blooming period (they begin to bloom one or two weeks after *M. heptapeta*), by the often continuous production of a few flowers until after the foliage has expanded, by the usual pink to purple coloration of the abaxial surfaces of the tepals, and by the generally larger size of the flowers. From *M. quinquepeta* the hybrids can be distinguished by their blooming period, by the usually petaloid outer whorl of tepals, by their mostly treelike habit, and by differences in the bases of the leaf blades.

Backcrosses between *Magnolia* × *soulangiana* and *M. quinquepeta* have been produced intentionally (represented in cultivation by cv. Dark Splendor, see Fogg & McDaniel, 1975), while successful pollinations have resulted in hybrids between *M.* × *soulangiana* and *M.* × *veitchii* as well (see D. T. Gresham, Morris Arb. Bull. 13: 48, 49. 1962).

Among the multitude of *Magnolia* × *soulangiana* cultivars, the following two were accounted for by Rehder (1940, 1949), are well known in cultivation, and are of historical interest: 'Lennei' (– *M.* × *soulangiana* var. *lennei* (Topf) Rehder in Bailey, Cycl. Am. Hort. 3: 966. 1901; *M. lenneana* Topf, Gartenflora 1: 86, 87; 244. 1852; see also N. Treseder. Newsl. Am. Magnolia Soc. 6(2): 5, 6. 1969), $2n = 114$, a plant with large suborbicular leaves and large, tulip-shaped flowers comprised of fleshy, obovate tepals flushed rosy-purple on the abaxial surfaces, the outer whorl sometimes sepaloid; and 'Rustica Rubra' (= *M.* × *soulangiana* f. *rubra* (Nicholson) Rehder, Jour. Arnold Arb. 21: 276. 1940; var. *rustica* Rehder in Bailey, Std. Cycl. Hort. 4: 1969. 1916; *M. rustica rubra* Nicholson, Flora Sylva 1: 17 + *pl.* 1903), a plant thought to be a seedling of 'Lennei' with shorter, broader tepals flushed clear, rosy-red, not purplish. For descriptions of numerous other cultivars of *M.* × *soulangiana* reference should be made to Bean (1973, pp. 666–668), *Hilliers' Manual* (1973, pp. 183, 184), and the complete listing in Fogg and McDaniel (1975).

2. **Michelia** Linnaeus, Sp. Pl. 1: 536. 1753; Gen. Pl. ed. 5. 240. 1754.

Evergreen trees or shrubs similar to *Magnolia* in structure and appearance; buds enclosed by stipular scales, leaving annular scars on the branchlets. Leaves alternate, petiolate, stipulate, the stipules caducous, adnate to the petioles (leaving obscure to conspicuous scars on the adaxial surfaces of the petioles) or free; leaf blades coriaceous, with entire margins, cuneate to rounded bases, and obtuse, acute, or acuminate apices. Flowers usually fragrant, axillary, solitary, short to long-pedicellate. Perianth generally cup-shaped, comprised of 6–21 subsimilar (or rarely ± dimorphic) fleshy tepals, in bud enclosed by stipular scales. Stamens numerous, the filaments usually very short, hardly differentiated from the elongated connectives, the connectives usually produced into acute or acuminate appendages; anther sacs elongate, dehiscing laterally or sublaterally. Gynoecia conspicuously stipitate, of numerous carpels (or rarely reduced to a single carpel), the carpels with 2 or more ovules, the stigmatic surfaces decurrent along the stylar beaks. Fruits conelike aggregates of free and lax or occasionally concrescent, longitudinally dehiscent follicles. Seeds 2 or more per follicle, like those of *Magnolia*. (*Champaca* Adanson; *Liriopsis* Spach.) TYPE SPECIES: *M. champaca* L. (Name commemorating Peter A. Michel, 1679–1737, a Florentine botanist.) — MICHELIA.

About 45 species of tropical and warm-temperate climates of southeastern Asia, India, and Ceylon. One species more commonly encountered in warmer areas of North America is precariously hardy in the southern part of our range, while *Michelia doltsopa* Buch.-Ham. ex DC., of western Yunnan, Tibet, and the eastern Himalayan region, and *M. compressa* (Maxim.) Sarg., of Japan, the Ryukyu Islands, and Taiwan, are sometimes grown in warmer regions of the United States. The flowers

of *M. champaca*, a large tree native to India, are the source of champaca oil, which is widely used in India as a perfume.

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1. **M. figo** (Loureiro) Sprengel in Linnaeus, Syst. Veg. ed. 16. 2: 643. 1825.

Bushy evergreen shrubs to ca. 6 m.; new growth covered with a coppery-colored pubescence, the young branchlets rufous-tomentose, older branchlets with finely fissured, grayish-brown bark. Petioles short, (1–)2–4 mm. long, finely rufous-pubescent; leaf blades thinly coriaceous, 3–8(–10) cm. long, 2–3.5(–4) cm. wide, elliptic to oblanceolate or obovate, usually constricted distally, tapering to the rounded or blunted apices, the bases cuneate; upper surfaces of the blades bright glossy green, the lower surfaces dull green, with prominent, often pubescent midveins. Flowers very fragrant, solitary, axillary, on short, pubescent pedicels, in bud enclosed by a single rufous-pubescent stipular bud scale; tepals 6, subsimilar, creamy white, yellowish, often tinged brownish-purple, oblong-ovate, 1.8–2.5 cm. long; stamens 7–10 mm. long, the connectives produced into obsolete acute appendages or the appendages absent; gynoecia distinctly stipitate, the gynophore and 2-ovulate carpels pubescent. Fruit aggregates 2–4 cm. long, cylindric, usually asymmetrical from seed abortion, the individual follicles free, dehiscing widely, the valves with short stylar beaks; seeds 2 per follicle, subglobose to globose, 8–10 mm. long, the outer seed coats red. $2n = 38$. (*Liriodendron figo* Lour.; *Magnolia fuscata* Andr.; *Liriopsis fuscata* (Andr.) Spach; *Michelia fuscata* (Andr.) Wall.) — BANANA-SHRUB.

Native to southeastern China; known to be cultivated in our area at Colonial Williamsburg, Virginia.

Tribe LIRIODENDREAE Reichenbach

3. Liriodendron Linnaeus, Sp. Pl. 1: 535. 1753; Gen. Pl. ed. 5. 239. 1754, "*Liriodendrum*." [6]

Deciduous trees of sympodial growth, the grayish bark becoming fissured into longitudinal platelets; young branchlets with septate pith; winter buds obovoid, enclosed by 2 coherent stipules, the terminal buds often mixed, containing a terminal flower primordium subtended by one or more axillary buds. Leaves alternate, long-petiolate, stipulate, the stipules free from the petioles, large and conspicuous, caducous, leaving annular scars at the nodes; leaf blades usually with a truncate or widely emarginate apex and 1 or 2 lateral lobes on each side near the base. Flowers odorless, appearing with the leaves, terminal, solitary. Perianth of 9 segments, 3 reflexed sepals forming the outer whorl, the inner 6 petals in 2 whorls of 3, simulating a campanulate or tuliplike corolla. Stamens numerous, spirally arranged, with stout filaments, the linear anther sacs extrorsely dehiscent, the connectives produced into apiculate appendages. Gynoecia sessile, of numerous spirally arranged, 2-ovulate carpels densely imbricated on an elongate axis; styles elongate, broad and flattened, constricted terminally into a small, ± recurved stigma. Fruit a spindle-shaped, brown, conelike aggregate of free, tightly imbricated, 2-seeded samaras deciduous at maturity, the floral axis persistent. Seeds small, with a thin, dry, seed coat; embryo embedded in endosperm. (*Tulipifera* Miller.) TYPE SPECIES: *L. tulipifera* L. (Name from Greek *lirion*, lily, and *dendron*, tree, in reference to the lily- or tuliplike flowers.)

Two species, one of eastern North America, the second of China and northern Indochina. Fossils indicate that the genus was widely distributed in temperate regions of the Northern Hemisphere during the Tertiary period. Recently, hybrids between the two species have been obtained as the results of intentional cross-pollinations (see F. S. Santamour, Jr., 1971, 1972).

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KEY TO THE SPECIES OF LIRIODENDRON

1. Petals 4–6 cm. long, with an irregular orange band near the base on both surfaces; gynoecium included within the perianth following anthesis. . . . . 1. *L. tulipifera.*
1. Petals 2–4 cm. long, green with yellow veins on the abaxial surface; gynoecium exserted from the perianth following anthesis. . . . . 2. *L. chinense.*

1. L. tulipifera Linnaeus, Sp. Pl. 1: 535. 1753. FIGURE 6, h–s.

Large trees to 50 m. or rarely to 60 m., the bark becoming deeply furrowed; branchlets ± stout, glabrous, brittle, reddish-brown and often ± glaucous, becoming grayish, the periderm exfoliating in thin sheets. Petioles 5–10 cm. long, the large caducous stipules up to 3.5 cm. long; leaf blades becoming golden yellow in fall, variable in outline, 7–12 cm. long, usually saddle–shaped, with 2 pairs of lateral lobes near the base and with 2 lobes distally, creating a ±truncate or shallowly emarginate apex, the lobes usually ± rounded, the juvenile leaf blades deeply lobed halfway or more to the middle; upper surfaces of the leaf blades bright green, the lower pale green, faintly glaucescent. Flowers ± tulip-shaped, the 3 outer sepals greenish, strongly reflexed, the inner 6 petals ± erect, 4–6 cm. long, 1.8–3 cm. wide, pale green, with an orange-colored band near the base, the color strongest on the adaxial surfaces; stamens numerous, usually included; filaments 10–15 mm. long, the anther sacs 15–25 mm. long; gynoecia mostly included, the carpels numerous, pale yellowish-green at anthesis. Fruit aggregates to 7 cm. long, the samaras light brown, ca. 5 mm. wide, to 4.5 cm. long, with acute apices, the lowermost samaras often persistent on the floral axis through winter. $2n = 38$. — TULIP-TREE, YELLOW-POPLAR, TULIP-POPLAR.

FIGURE 6. **Liriodendron.** a–g, *L. chinense*: a, habit of flowering branchlet, × ¾; b, petal, × ½; c, abaxial view of stamen showing extrorse lines of anther sac dehiscence, × 1½; d, samara, × 1; e, seeds as positioned in samara, × 3; f, outline of typical leaf, × ¼; g, outline of juvenile leaf, × ⅙. h–s, *L. tulipifera*: h, habit of flowering branchlet, × ½; i, petal showing band of orange pigmentation, × ½; j, abaxial view of stamen, × 1½; k, flower with perianth

Native to the deciduous forests of eastern North America from Massachusetts, Vermont, and southern Ontario southward to eastern Missouri, Arkansas, Louisiana, and Florida. (See E. L. Little, Jr., Atlas U. S. Trees 1: *Map 137-E.* 1971.)

Numerous variants of *Liriodendron tulipifera* have been recognized in cultivation. Several variants which probably occur sporadically in nature have also been given botanical names at the rank of variety or forma. Most, however, have subsequently been treated as cultivars, and they are listed as such below. However, should reference to these variants in a botanical context be preferred or necessary, the equivalent botanical names are given in parentheses. Among the variants are 'Aureomarginatum' (= *L. tulipifera* f. *aureomarginatum* Hort. ex Schelle in Beissner *et al.*, Laubh.-Ben. 101. 1903), plants with the leaf blades edged yellow or greenish-yellow; 'Fastigiatum' (= *L. tulipifera* var. *fastigiatum* H. Jäger in Jäger & Beissner, Ziergeh. ed. 2. 203. 1884; *L. tulipifera* f. *fastigiatum* Schelle ex Schwerin, Mitt. Deutsch. Dendr. Ges. 1919: 140. 1919; *L. tulipifera* f. *fastigiatum* Schelle, nomen nudum), erect trees of columnar habit; 'Integrifolium' (= *L. tulipifera* f. *integrifolium* Kirchner in Petzold & Kirchner, Arb. Muscav. 118. 1864, without indication of rank; rank assigned by Schwerin, Mitt. Deutsch. Dendr. Ges. 1919: 140. 1919), plants with the leaf blades lacking lower, lateral lobes; and 'Obtusilobum' (= *L. tulipifera* var. *obtusilobum* Michx., Fl. Bor.-Am. 1: 326. 1803; *L. tulipifera* f. *obtusilobum* (Michx.) Schelle in Beissner *et al.*, Handb. Laubh.-Ben. 101. 1903), plants having leaf blades with one rounded lobe at each side near the base. Additional cultivars of *L. tulipifera* are listed and described in Bean (1973, p. 586) and Krüssmann (1960, p. 63).

2. **L. chinense** (Hemsley) Sargent, Trees & Shrubs **1**: 103. *t. 52.* 1903.
FIGURE 6, a–g.

Trees to ca. 16 m., similar in structure and appearance to *Liriodendron tulipifera* but apparently not attaining the size of that species. Petioles 7–18 cm. long, the caducous stipules to 3.5 cm. long; leaf blades variable in outline, usually saddle-shaped, with 1 pair of lateral lobes near the base and with 2 lobes distally, creating a ± truncate or shallowly emarginate apex, the lobes usually drawn out and ± apiculate, the juvenile leaf blades deeply lobed halfway or more to the middle, the lobes not apiculate; upper surfaces of the blades dark green, the lower surfaces glaucescent. Flowers ± cup-shaped, the 3 outer sepals greenish, reflexed, the 6 inner petals ± erect, 3–4 cm. long, glaucescent and green on the abaxial surfaces, green with yellow veins on the adaxial surfaces; stamens nu-

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and stamens removed to show gynoecium, × ½; l, detail of apex of carpel showing stigma, × 6; m, conelike aggregate of samaras, × ½; n, samara, × 1; o, seeds as positioned in samara, × 3; p, q, r, outlines of leaves showing variation in shape, × ¼; s, outline of juvenile leaf, × ⅙.

merous, about as long as the tepals, the filaments 5–7 mm. long, the anther sacs 10–16 mm. long; gynoecia exserted at anthesis, the carpels numerous, yellowish-green. Fruit aggregates to 9 cm. long, the light brown samaras ca. 6 mm. wide, to 4 cm. long, the outer (lower) samaras usually with acute apices, the inner (upper) samaras with acute or usually obtuse apices. $2n = 38$. (*L. tulipifera* var. ? *chinense* Hemsley; *L. tulipifera* var. *sinensis* Diels.) — CHINESE TULIP-TREE.

Native to China and Indochina. Recent distribution records (see C. Y. Wu & W. T. Wang, Acta Phytotax. Sinica 6: 183–254. *pls. 45–50.* 1957) indicate its occurrence in Anhwei, Kiangsi, Fukien, Hupeh, Szechwan, Kweichow, Kwangsi, and Yunnan provinces, China, and in Chapa, Vietnam.

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THE MONTANE FORESTS AND SOILS OF JAMAICA: A REASSESSMENT

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WHEN FORREST SHREVE published his account of the forests of the Blue Mountains of Jamaica in 1914, it represented a landmark in the study of forests on tropical mountains. His detailed floristic and ecological account brought out the differences between ridges, slopes, and gullies and between windward and leeward sides of the range. He considered the forests particularly in relation to water supply, made comparative microclimatic records, and carried out simple experiments on certain species characteristic of ridge or gully sites. No detailed study of the forests has been made since his time, and nothing substantially new was added to his account of the Blue Mountain forests by Asprey and Robbins (1953) in their synopsis of the vegetation of the whole island.

Since Shreve's time, descriptions of the forests on many tropical mountains have been published, and it has been found possible to assign most of the forests to a small number of formation types on the basis of structure and physiognomy (cf. TABLE 1). The emphasis in interpretation of the factors limiting the distributions of forest types has moved away from almost exclusive reference to temperature and water relations, while the role played by differences in mineral supply has come to be appreciated more fully.

In the present paper we will show how the forests of the Blue Mountains and other major ranges in Jamaica fit into the world picture of formation types, and we will attempt to relate different forest types to different soil types. From the mountains of the Caribbean the formation of mor humus [1] will be described for the first time, as well as a distinct forest type that is associated with mor. Information from foliar analyses will also be used as a basis for discussion of the mineral factors limiting distributions.

This paper is based primarily on a reconnaissance made by both of us in December, 1973, in the Blue Mountains and Port Royal Mountains, but it incorporates some information gained by one of us (E. V. J. T.) during a year's detailed study of some of the sites visited then. It also includes the results of two reconnaissance trips by one of us (E. V. J. T.) to the John Crow Mountains in January and March of 1975.

[1] Mor humus is defined as humus which rests on the top of the mineral soil and is mixed with the mineral soil to a negligible degree; it is normally (perhaps always) very acid ($pH_{H_2O} < 4$, often ca. 3). Mull humus is defined as humus which is well mixed with the mineral material in the soil profile; the pH_{H_2O} varies from > 7 to < 4, but is usually > 4.

TABLE 1. **Characters generally used in defining forest formation types on wet tropical mountains.***

FORMATION TYPE	LOWLAND RAIN FOREST	LOWER MONTANE RAIN FOREST	UPPER MONTANE RAIN FOREST	SUBALPINE RAIN FOREST
HEIGHT OF FOREST †	25–45(–67) m.	15–33(–45) m.	1.5–18(–26) m.	1.5–9(–15) m.
DOMINANT LEAF-SIZE CLASS ‡ OF TREES AND SHRUBS	*Mesophyll*	*Notophyll or Mesophyll*	*Microphyll*	*Nanophyll*
BUTTRESSES ON TREES	*Usually frequent and large*	*Infrequent or small or both*	Usually none	None
CAULIFLOROUS TREE SPECIES	Frequent	Rare	None	None
COMPOUND LEAVES ON TREES	*Abundant*	Occasional	Few	None
DRIP-TIPS ON LEAVES	*Abundant*	Frequent or occasional	Few or none	None
CLIMBERS	*Thick-stemmed woody species frequent*	*Thick-stemmed woody species usually none; other species often frequent*	Usually very few	Very few
VASCULAR EPIPHYTES	Frequent	*Abundant*	Frequent	Occasional

* Based on the system of Richards (1952), variously revised up to the time of Grubb and Stevens (in press); the most useful characters in italics.

† Emergents in parentheses.

‡ According to the systems of Raunkiaer (1934) and Webb (1959).

STUDY AREAS

THE BLUE MOUNTAINS. These run from east to west in the eastern part of Jamaica (FIGURE 1) and rise to 2265 meters. We studied two areas familiar to Shreve, that at about 1500 to 1600 meters west of Morce's Gap (northwest of Cinchona) and that above 1600 meters along the main route to the highest summit, Blue Mountain Peak, via Portland Gap (FIGURE 1). The geology of the range is complex, including granodiorite, "Blue Mountain Volcanics," "Blue Mountain Shales" (mudstones, sandstones, and conglomerates), and massive Eocene limestone in the first of the areas, and "Blue Mountain Volcanics" and "Shales" in the second (unpublished provisional map of Jamaican Geological Survey). According to Shreve, the annual rainfall is about 3300 mm. at sea level on the north side of the range, about 4270 mm. on Blue Mountain

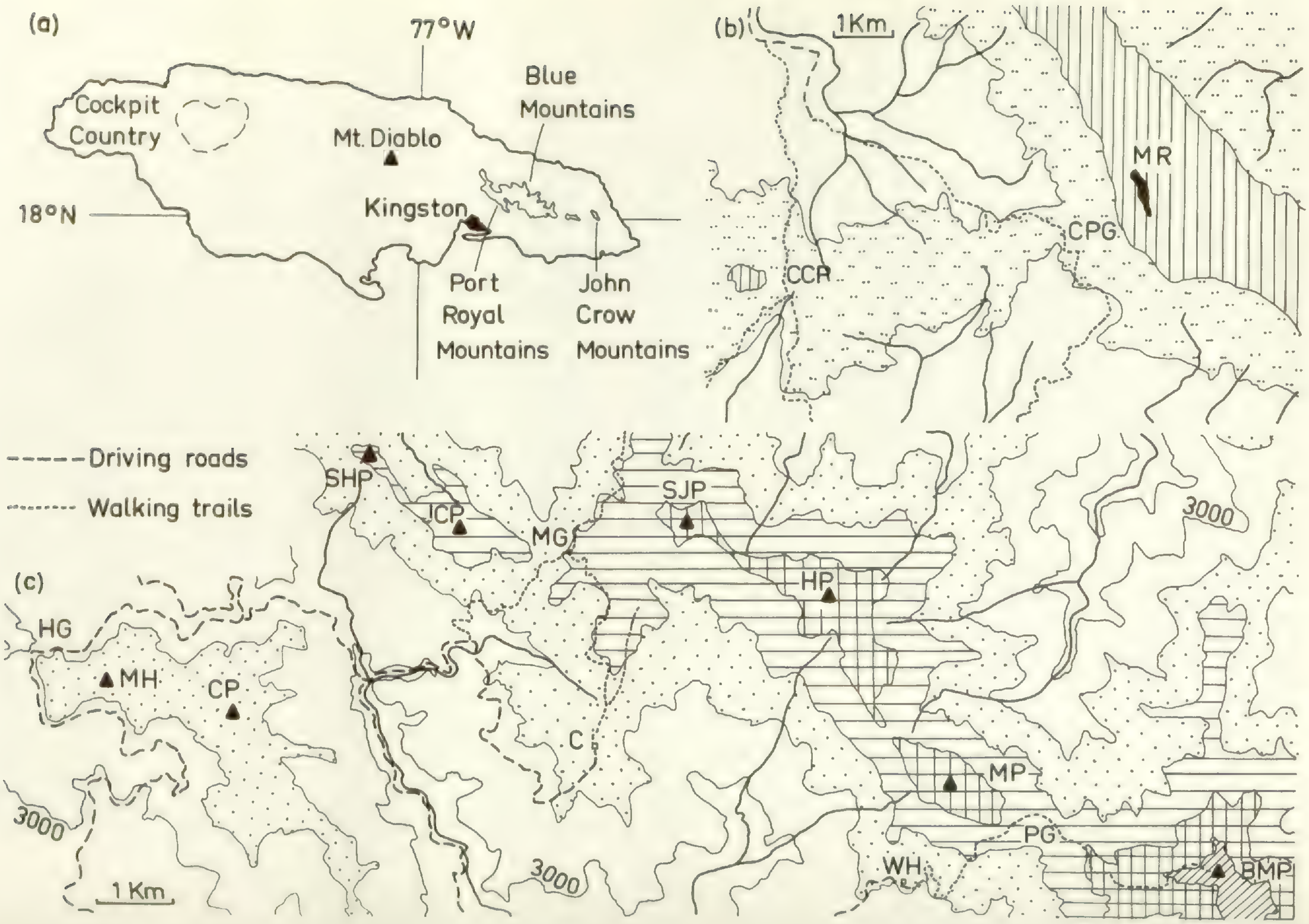
Peak, about 2690 mm. at Cinchona (1500 m. alt.) on the south side, and about 2890 mm. at New Haven Gap at 1705 meters on the main divide. The rainfall is markedly seasonal and the wettest months are August to December and May to June. The northern slopes are windward to the North East Trade Winds, and there is a marked rain shadow effect on the southern slopes. The northern slopes, which are much more often in cloud, are still largely forested. However, the drier and sunnier southern slopes were extensively cleared for the planting of coffee in the past (though they are mostly used for subsistence farming now), and only small patches of disturbed forest remain. *Pinus caribaea* Morelet [2] has been planted extensively by the Forest Department in certain areas (e.g., west of Cinchona), while scattered groves of *Eucalyptus* species also contribute significantly to the overall appearance.

Many plants have been introduced at the Botanic Garden at Cinchona, but few have spread for any distance into the indigenous communities. *Hedychium gardneranum* (from the Himalayas) is frequent along the trail to Morce's Gap on wetter slopes and in gullies. Quinine trees (*Cinchona pubescens*, *C. officinalis*, and hybrids), introduced from Peru, have spread into patches of relatively undisturbed DRY SLOPE forest along the track to Morce's Gap. *Pittosporum undulatum* (from southeast Australia) is very frequent as an established tree along the trail to Morce's Gap, and many seedlings were found on the trail to the north of the Gap on the windward slope. This species also invades the apparently undisturbed forest well away from the track; saplings were found in all four major forest types on the ridge leading to John Crow Peak. Copious seed is produced by plants along the track, and in a simple test it was found that 100 per cent germinated within 46 days.

THE PORT ROYAL MOUNTAINS. These run from northwest to southeast between the Blue Mountains and Kingston (FIGURE 1). We studied only Mt. Horeb (about 1450 meters), a "hog's back" ridge composed chiefly of "Newcastle Volcanics." The rainfall in this area is in the range of 1500 to 2500 mm. (Asprey & Robbins, 1953). The forest at the western end of Mt. Horeb is particularly interesting, because it is very frequently shrouded in clouds which roll around the western end of the Blue Mountains and on to Hardwar Gap on the western side of Mt. Horeb.

THE JOHN CROW MOUNTAINS. These run approximately north–south in the easternmost part of the island (FIGURE 1). They rise to 1100 meters and consist of tilted massive Eocene or Miocene limestone, with a scarp face on the western side. Ascents of the western side were made along a ridge from Corn Puss Gap (at about 650 meters) up to about 950 meters. There is no track, and the climb was made through continuous forest. The forest decreases in height steadily with the increase in altitude, but above about 950 meters a marked break was found, with the terrain becom-

[2] Unless otherwise indicated, nomenclature follows that of Adams (1972) and Proctor (1953).


(a)
77°W
Blue
Mountains
Cockpit
Country
Mt. Diablo
18°N
Kingston
Port
Royal
Mountains
John
Crow
Mountains
(b)
1Km
MR
CPG
CCP
-----Driving roads
------ Walking trails
SHP
ICP
MG
SJP
3000
HP
(c)
HG
MH
CP
C
MP
PG
WH
BMP
3000
3000
1 Km

ing distinctly steeper and more rugged. A closed canopy composed of trees rooted in the deep grykes [3] occurs between the huge outcropping rocks. The annual rainfall is said to be over 2500 mm. throughout the area, certainly over 5000 mm. at the northern end of the range and possibly over 7500 mm. (Asprey & Robbins, 1953). There are also said to be few rain-free days (C. D. Adams & G. R. Proctor, pers. comm.).

FOREST AND SOIL TYPES RECOGNIZED

Altogether ten forest types have been recognized (the names of which are also used here to designate soil types).

1. Mor Ridge forest. Characteristic of knolls on ridges; known only between Morce's Gap and Silver Hill Peak.
2. Mull Ridge forest. Widespread in the Blue Mountains up to about 1850 meters.
3. Wet Slope forest. Very extensive on the northern slopes of the Blue Mountains; also found just over the divide on the southern side (clouds frequently roll just over the edge from the windward side and then disappear); also present on the northern slopes of the Port Royal Mountains.
4. Gully forest. Widespread on northern and southern sides of the Blue Mountains up to about 1750 meters.
5. Very Wet Ridge forest. Known only from the frequently fogged end of Mt. Horeb in the Port Royal Mountains.
6. High Altitude forest. Found on slopes and ridges above about 1850 meters on Blue Mountain Peak; probably also on the other highest peaks.
7. Dry Slope forest. Widespread on the southern slopes of the Blue Mountains.
8. Dry Limestone scrub forest. Known only from the deeply dissected limestone outcrop at 1750 to 1800 meters on the southwest side of John Crow Peak in the Blue Mountains.

Figure 1. a, Outline map of Jamaica showing three main mountain ranges studied at the eastern end of the island; the contour is at 3000 ft. (915 m.). b, Details of the study area in the John Crow Mountains with areas above 2000 ft. (610 m.) and 3000 ft. (915 m.) shaded; CCP = Cuna Cuna Gap, CPG = Corn Puss Gap, MR = Main Ridge (> 3750 ft., 1143 m.). c, Details of Port Royal and Blue Mountain ranges with areas above 4000 ft. (1220 m.), 5000 ft. (1525 m.), 6000 ft. (1830 m.), and 7000 ft. (2135 m.) shaded. (BMP = Blue Mountain Peak; C = Cinchona; CP = Catharine's Peak; HG = Hardwar Gap; HP = High Peak; JCP = John Crow Peak; MG = Morce's Gap; MH = Mt. Horeb; MP = Mossman's Peak; PG = Portland Gap; SHP = Silver Hill Peak; SJP = Sir John Peak; WH = Whitfield Hall.) Based on the Ordnance Survey of Jamaica (1970).

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[3] Grykes are cracklike hollows formed in hard limestone having karst-type topography; they are commonly 1–2 m. deep and 10–50 cm. wide.

9. WET LIMESTONE forest (lower) and (10) WET LIMESTONE forest (upper). Studied at 770 to 950 meters in the John Crow Mountains and probably widespread there.

The topographical distribution of types 1 to 4 and type 8 on the ridge from Morce's Gap to John Crow Peak is shown in FIGURE 2.

Shreve did not report on the Port Royal or John Crow Mountains. His account of the forests in the Blue Mountains is in close agreement with ours in respect to the WET SLOPE, DRY SLOPE, and GULLY forests, and it is in reasonable agreement with ours concerning the HIGH ALTITUDE forest and DRY LIMESTONE scrub forest. However, we present here a strongly revised assessment of the RIDGE forests; Shreve appears to have overlooked the development of mor humus on certain ridge sites.

During our study of the Blue Mountain forests, we found most of the tree, shrub, and climbing species mentioned by Shreve, although we missed a few recorded only at or near Blue Mountain Peak or only in windward ravines, a habitat which we did not have time to study. We saw only one specimen of *Citharexylum caudatum* (in MULL RIDGE forest next to the track at Morce's Gap), which Shreve noted to be a species of leeward (i.e. dry) slopes. We did not find *Eugenia harrisii* or *Myrcianthes* (*Eugenia*) *fragrans* (although we recorded *E. monticola* and *E. virgultosa*); nor did we find *Miconia rubens* or *Psychotria "brownei"* (although we did find *M. theaezans* and *P. sloanei*). In addition, we recorded a few more species missed by Shreve: *Calyptranthes rigida*, *Conostegia montana*, *Haenianthus incrassatus*, *Ilex harrisii* and *I. sideroxyloides* (both close to *I. macfadyenii* = *"I. montana"* of Shreve), and *Maytenus jamaicensis*.

DESCRIPTIONS OF THE SOIL TYPES

In the Blue Mountains the soils occupying the greatest area are those of the WET SLOPE and DRY SLOPE forests, and the next most widespread are those of the MULL RIDGE and GULLY forests. These all have a moderate organic matter content; on the slopes (but not on the ridges or in the gullies) there are frequent stones close to the surface and occasionally quite large rocks. All of these soils are freely drained. During a year's study no standing water was ever seen and no water table encountered. Streams are not seen much above an altitude of 1200 meters in the drier months in the Cinchona area, but they reach up to 1500 meters in wet spells. No marked differences were found between soils derived from "shale" and volcanic formations or granodiorite. Earthworms and ants appeared to be very rare — just one earthworm was seen (in a GULLY forest soil). Cockroaches are frequent and may be important in the breakdown of litter (cf. Murphy, 1973). Other mesofauna (centipedes, millipedes, termites, etc.) were not recorded. Burrowing mammals (mongooses and rats) are occasional.

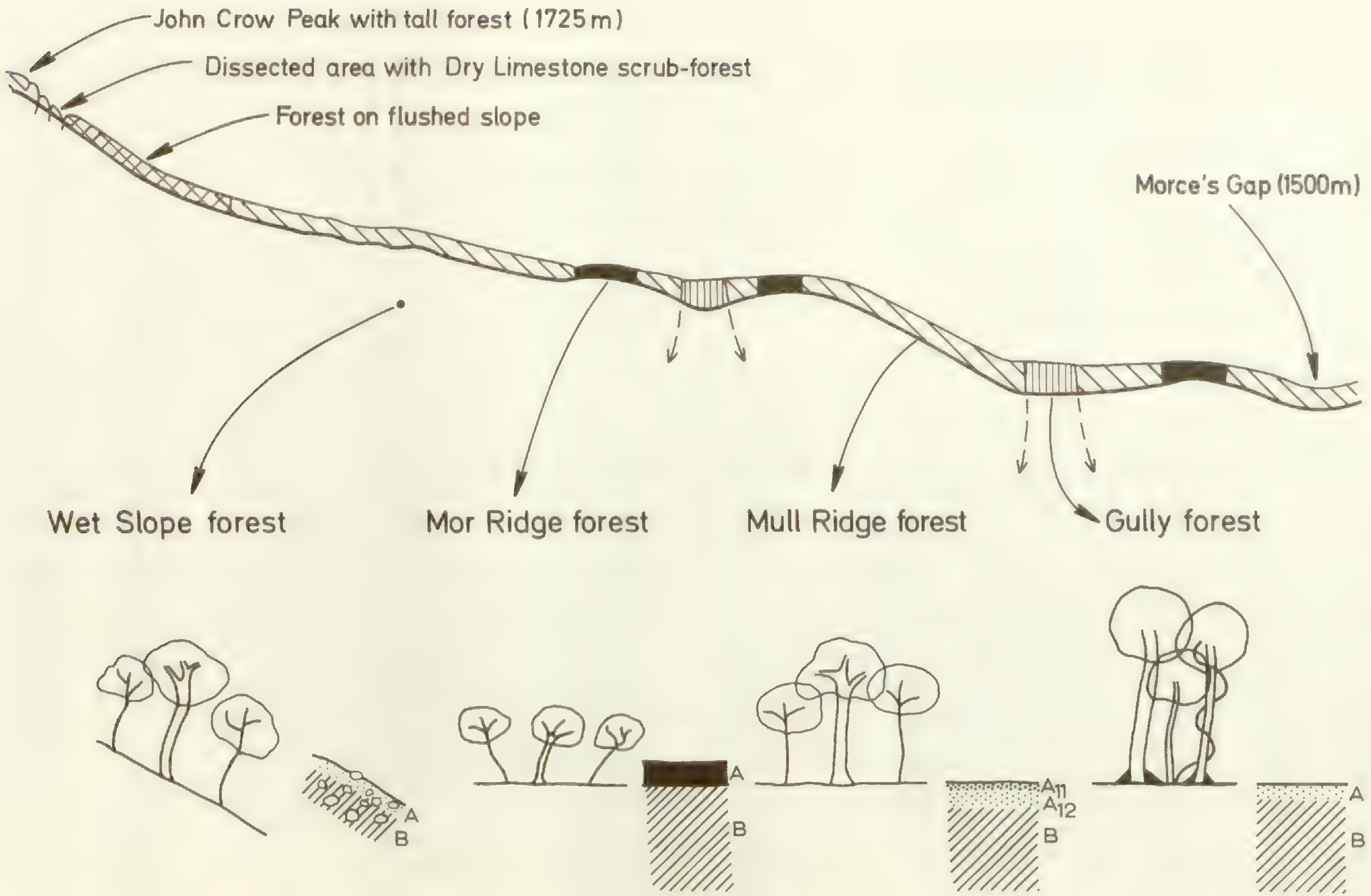

FIGURE 2. A transect of the ridge from Morce's Gap (east) to John Crow Peak (west) showing the main features of the four principal forest and soil types in the area.

The following is a generalized profile of a WET SLOPE forest soil.

A_{00}	5/1–0 cm.	Discontinuous litter (L) layer; F layer very thin.
A	0–10 cm.	Brown clay-loam with stones. Not obviously or markedly enriched in organic matter. Fine roots abundant. pH 4.0–4.5.[4] Loss-on-ignition (48 h at 375°) about 16 per cent dry weight.
B	10–30 cm. +	Yellowish clay with abundant stones and large rocks which are so dense that it is difficult to dig below 30 cm.

The WET SLOPE forest soils are clearly immature and are probably best classified as lithosols.

No detailed study was made of the DRY SLOPE forest soils, but they resemble the WET SLOPE soils in general character.

A generalized profile of a MULL RIDGE forest soil is as follows.

A_{00}	2/1–0 cm.	Continuous litter (L) layer; F layer very thin.
A_{11}	0–5/10 cm.	Dark brown clay-loam with poorly developed crumb structure; cannot be molded into a ball with the fingers. Fine roots abundant; few at surface. pH 3.5–4.0. Loss-on-ignition ca. 36 per cent.
A_{12}	5/10–20 cm.	Brown clay-loam with less organic matter and poorer structure. Color and texture like "A" horizon of slope soils. Roots fewer and larger. pH 3.9–4.6.
B	20–80 cm. +	Yellowish clay which can just be molded into a ball. Becomes paler with depth, with increasing numbers of rock fragments. Few roots below 30 cm. pH ca. 4.5–6.0.

The MULL RIDGE forest soils have developed to a stage more mature than that of a lithosol, but in the absence of mineralogical data it is not possible to classify them. However, they are in several respects like the base-poor brown earths and brown podzolic soils of the North Temperate Zone.

[4] All pH values reported in this paper are based on measurements made electrometrically on soil samples brought to a paste with distilled water. All pH values quoted from other papers without comment are based on some sort of measurement in distilled water.

The GULLY forest soils differ from the MULL RIDGE forest soils in their discontinuous litter cover, lesser organic enrichment of the mineral topsoil, and higher pH. A generalized profile is as follows.

A_{00}	2/1–0 cm.	Discontinuous litter (70 per cent cover); F layer very thin.
A_{11}	0–(1/3) cm.	Dark brown clay-loam with poor crumb structure. Fine roots abundant. pH 4.4–5.0(–6.2). No sharp boundary to A_{12}.
A_{12}	(1/3)–(10) cm.	Brown clay-loam with still poorer crumb structure. Fine roots abundant. No sharp boundary to B. pH 4.5–4.9. Loss-on-ignition for soil at 0–10 cm. ca. 36 per cent.
B	(10)–70/100 cm. +	Yellow brown clay becoming slightly paler below. Few roots below 25 cm. pH 4.5–6.0.

Much more restricted in distribution are the MOR RIDGE forest soils. These differ from the MULL RIDGE forest soils in an opposite way from the GULLY forest soils, having a very deep and almost wholly organic H layer and a lower pH. A generalized profile is as follows.

A_{00}	1–2 cm. thick.	Litter (L) layer continuous.
A_0	20–50 cm. thick.	Deep reddish brown, minutely granular, not coherent, not greasy; leaf fragments and living roots throughout. The lowest 10 cm. have a mineral component. pH 2.8–3.5(–3.8). No regular change in pH with depth. F and H layers not distinct. Loss-on-ignition ca. 96 per cent.
?B	Up to at least 100 cm. thick.	Abrupt transition (1–2 cm. deep) to yellowish clay which is sticky and can be molded. Almost no roots. Rock fragments at base. Generally no eluviated or cemented horizons. An A_e layer (pale gray-brown clay, 2–3 cm. thick) and a B_H layer (black-brown. cemented 1 cm. thick) were detected once but not refound. pH 4.5 (3 samples).

There appeared to be no mesofauna in the mor. However, the burrows of rats are quite common and mongooses are also present. The rats also nest in the trees.

The fully developed mor profile is easy to detect, because the soil is distinctly springy to walk on. However, many sites were found with early stages of mor development, indicating a continuum with the MULL RIDGE forest soils. Since there is no regular evidence of eluviated or very markedly illuviated horizons, the soils cannot be classified as podzols, and there is indeed no generally recognized world group of soils to which they can be assigned.

The mor humus might be termed peat by a casual observer. However, for a number of reasons presented in the discussion, we believe that this designation would be incorrect.

The VERY WET RIDGE forest soil on Mt. Horeb is quite unlike the MOR RIDGE forest soil and is indeed more like the GULLY soil type by virtue of its having only the top 1 to 2 cm. of the mineral soil markedly humus-enriched, dark brown, and with a strong crumb structure (pH 4.2). This soil differs from the GULLY forest soil in its 100 per cent litter cover. Below the humus-enriched layer the soil is first midbrown with much weaker crumb structure (pH 4.5), then paler and yellowish (pH 4.8).

The HIGH ALTITUDE forest soils studied were all on steep slopes or on the top of a knife-edge ridge. In general character they resemble the WET SLOPE forest soils. However, they vary a good deal in depth and in the apparent degree of enrichment with humus; above 2000 meters the soils derived from shales appeared to have a more marked crumb structure than those derived from tuffs. One earthworm was seen. The pH at 0 to 3 cm. and at 8 to 10 cm. is generally 4.1–5.9 (mean 4.8 at 0 to 3 cm., 5.0 at 8 to 10 cm., 14 sites recorded).

The WET LIMESTONE forest soils of the John Crown Mountains consist of sticky yellowish-brown clays 20 to 30 (to 50) cm. deep. There is a continuous litter cover, and the upper 10 cm. of the mineral soil are clearly enriched with humus (loss-on-ignition 17 to 37 per cent). The profile is heavily leached, since the pH throughout is 4.5–4.8, and it thus resembles that reported by Asprey and Robbins (1953, p. 387) from the bauxite areas developed over limestone farther west. Very surprisingly, in view of the present climate, the soil seems more similar to a Terra Fusca than to a Rendzina.

The soil of the DRY LIMESTONE scrub forest on the southeast slope of John Crow Peak, just below the summit, differs from that just described in its color (reddish-brown), in its lack of any obvious humus enrichment, in its being less leached (pH 6.4–6.8), and in its being generally shallower, most often 3 to 4 cm. deep (0 to 12 cm. in extremes). In addition, it has a marked clay-loam texture and a weak crumb structure. The litter layer is thin and discontinuous except under the denser stands of the bamboo *Chusquea abietifolia*. The obvious affinity of the soil is with the Terra Rossas.

We may summarize the salient points about the several soil types as follows. The SLOPE forest soils, whether wet or dry and whether at high altitudes or low, are lithosols moderately to strongly acid at the surface

(pH mostly 4.0–5.5), while the more stable soils of the MULL RIDGE forest (at least in the Morce's Gap area) are deeper, less stony, and more mature, with a distinct accumulation of humus in the top 10 cm. and a surface pH of 3.5–4.0. The end point in this leaching series is found in the MOR RIDGE forest soils of knolls on the ridges where an H layer up to 50 cm. thick is found, and the pH throughout is 2.8–3.5(–3.8). The GULLY forest soils are also deeper and less stony than the SLOPE soils, but they have a discontinuous litter layer, and obvious humus enrichment extends to a depth of only 1 to 3 cm. (pH 4.4–5.0). The VERY WET RIDGE forest soil on Mt. Horeb is much more like the GULLY forest soil than the MOR RIDGE forest soil but is a little more acid (topsoil pH 4.2). The WET LIMESTONE forest soils are highly leached, moderately rich in organic matter, and in the same pH range as lithosols on nonlimestone rocks. The DRY LIMESTONE scrub forest soil is much shallower than that of the WET LIMESTONE forest, redder, and much less leached (pH 6.4–6.8); it also has a more loamy texture.

DESCRIPTIONS OF THE FOREST TYPES

The following account is of a preliminary nature and much further research needs to be done. A quantitative analysis of the composition and dynamics of the first four forest types listed in TABLE 2 will be given in a later publication.

It is convenient to deal with the forests in a somewhat different order from the soils, beginning with one of the types poorest in species.

MOR RIDGE forest. This has a rather open canopy (4 to)5 to 7 meters tall, made up of trees of small girth (mostly less than 30 cm. DBH). Almost all of the larger trees are leaning, apparently because of the poor support offered by the deep humus layer in which nearly all of the roots occur. The trees presumably develop their crowns a little unevenly and, when these become heavy, the roots fail to provide the resistance to displacement that is provided by roots in a firm, mineral soil. The trees in the MOR RIDGE forest lean in all directions, and windthrow does not seem to be involved. (It is significant that few of the trees in the MULL RIDGE forest lean over.) Sixteen dicotyledonous tree species were recorded (TABLE 2), three of them only once. Tree ferns are much less common and smaller than in the other forest types in the area — only two species are present (TABLE 3). The shrub layer is very poorly developed and contains only two species (both melastomes); *Blakea trinervia* is a scrambling species up to 4 meters tall, while *Miconia rigida* is upright and grows to about 2 meters.

The dicotyledonous tree species fall into two main groups, the "core" species found in gullies and on slopes, as well as on ridges, and a group confined to ridges and slopes (TABLE 2). None were found to be exclusive to MOR RIDGE forest in the Morce's Gap area. However, as shown in TABLE 3, the two tree ferns and the two shrubs are exclusive

FIGURE 3. **Mor Ridge forest.** Scale pole marked in feet. Sapling on left is *Lyonia* cf. *octandra*. Most bromeliads are *Tillandsia complanata* or *Vriesia sintenisii*; the one in flower is *Vriesia sintenisii*. February, 1975. Photo by E. V. J. Tanner.

to MOR RIDGE forest in this area; *Blakea trinervia* is often epiphytic elsewhere, and *Miconia rigida* is found elsewhere in VERY WET RIDGE forest and in HIGH ALTITUDE forest.

About half the "herb layer" (0 to 50 cm.), in terms of individuals, is made up of tree seedlings, and there are few herbaceous, regularly ground-dwelling species (TABLE 3). By far the most abundant are *Elaphoglossum latifolium* and *Peperomia* cf. *clusiifolia*, both somewhat succulent. In addition, it is characteristic of this forest type that several primarily epiphytic species are frequently found growing on the forest floor: the woody scrambler *Columnea hirsuta* (Gesneriaceae) and the orchids *Dichaea*

TABLE 2. Trees (other than tree ferns) present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains.*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Core species											
Alchornea latifolia	No	+	+	+	+	+	–	+	–	–	+
Clethra occidentalis	No	+	+	+	+	+	–	+	(+)	–	+
Clusia havetioides	No	+	+	+	+	+	–	+	(+)	+	+
Cyrilla racemiflora	Mi	+	+	+	+	+	+	+	–	+	–
Ilex macfadyenii	Mi	+	+	+	+	+	+	+	–	–	–
Podocarpus urbanii	Na	+	+	+	+	+	+	(+)	(+)	–	–
Mor Ridge species (mostly also on Mull Ridges and some on Wet Slopes)											
Chaetocarpus globosus	Mi	+	+	(+)	–	+	–	–	–	–	–
Ilex obcordata	Na	+	(+)	(+)	–	+	+	+	–	–	–
Lyonia jamaicensis + *L. octandra*	Mi	+	+	+	–	(+)	(+)	+	–	–	–
Mecranium purpurascens	Mi	+	+	–	–	–	(+)	(+)	–	–	–
Persea alpigena	No	+	+	–	–	–	–	–	–	–	–
Schefflera sciadophyllum	Me	+	+	–	–	(+)	(+)	–	–	+	–
Vaccinium meridionale	Mi	+	+	+	–	+	+	+	–	–	–
Mull Ridge and Wet Slope Species (mostly extending to Gullies)											
Brunfelsia jamaicensis	Mi	–	+	+	+	–	–	(+)	+	–	–
Bumelia montana	Mi	–	+	+	+	–	–	–	–	–	–
Calyptranthes rigida	Mi	–	+	+	+	–	–	–	–	–	–

TABLE 2. Trees (other than tree ferns) present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains (*continued*).*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Cleyera theaeoides	Mi	–	+	+	+	–	–	–	–	–	+
Conostegia montana	No	–	+	+	+	–	–	–	–	+	+
Dendropanax arboreus	Me	–	–	(+)	–	–	–	–	–	–	–
D. pendulus + *D. nutans*	No	–	+	+	+	+	+	+	(+)	?	?
Eugenia marchiana	No	–	+	+	+	?	–	–	–	–	–
E. monticola	Mi	–	+	+	+	?	–	–	–	–	–
E. virgultosa	Mi	–	+	+	+	?	(+)	–	–	–	–
Eupatorium critoniforme	No	–	+	+	+	–	–	–	–	+	–
Gesneria alpina	Mi	–	–	(+)	–	–	–	–	–	–	–
Guarea swartzii	No	–	+	+	+	+	–	–	–	+	+
Haenianthus incrassatus	Mi	–	+	+	+	+	–	–	–	+	–
Hedyosmum arborescens	No	–	+	+	+	+	–	–	–	+	+
Ilex harrisii	Mi	–	+	+	–	–	–	–	–	–	–
I. sideroxyloides	Mi	–	+	+	–	–	–	–	–	–	–
Maytenus jamaicensis	Mi	–	+	+	–	–	–	–	–	–	–
Meriania leucantha	No	–	+	+	+	–	–	–	–	–	+
Miconia theaezans	No	–	+	+	–	+	–	+	–	–	–
Nectandra patens	No	–	–	(+)	–	–	–	–	–	–	–
Piper arboreum	Me	–	+	+	+	–	–	–	–	–	+
Xylosma nitida	No	–	–	(+)	–	–	–	(+)	–	–	–
Gully species (extending to Slopes; rarely Ridges)											
Laplacea haematoxylon	Mi	–	(+)	+	+	(+)	–	–	–	+	+
Meriania purpurea	Mi	–	(+)	(+)	+	–	(+)	–	–	–	–
Psychotria sloanei	Mi	–	–	+	+	–	–	–	–	–	–
Solanum punctulatum	No	–	+	+	+	–	–	–	–	–	–
Turpinia occidentalis	No	–	(+)	+	+	–	–	–	–	–	–
High Altitude species											
Clethra alexandri	Me	–	–	–	–	–	+	–	–	–	–
Eugenia alpina	Na	–	–	–	–	–	+	–	–	–	–
Senecio swartzianus	Ma	–	–	–	–	–	+	–	–	–	–
Dry Slope species											
Brunellia comocladiifolia	No	–	(+)	–	–	–	(+)	+	–	–	–
Cestrum diurnum var. *odontospermum*	No	–	–	–	–	–	–	(+)	–	–	–
Daphnopsis americana	No	–	–	–	–	–	–	+	–	–	–
Dodonaea viscosa	Mi	–	–	–	–	–	–	+	–	–	–
Garrya fadyenii	Mi	–	–	–	–	–	+	+	+	–	–
Juniperus barbadensis	Le	–	(+)	(+)	–	–	–	+	–	–	–
Miconia quadrangularis	No	–	–	–	–	–	(+)	+	+	–	–
Myrica cerifera	Mi	(+)	(+)	(+)	–	–	(+)	+	–	–	–
Myrsine coriacea	Mi	(+)	(+)	–	–	–	–	+	+	–	–
Oreopanax capitatus	Me	–	–	–	–	–	–	+	–	+	–
Rhamnus sphaerospermus	No	(+)	(+)	–	–	–	+	+	–	–	–
Viburnum alpinum	Mi	–	(+)	(+)	–	–	+	+	–	–	–
V. villosum	Mi	–			–	–		+	–	–	–
Species of scrub forest on Dissected Limestone											
Fagara hartii	Mi	–	–	–	–	–	–	–	+	–	–

TABLE 2. Trees (other than tree ferns) present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains (*continued*).*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Myrcia sp.	Na	–	–	–	–	–	–	–	+	–	–
Weinmannia pinnata	Na	–	–	–	–	(+)	(+)	–	+	–	–
Wet Limestone forest species											
cf. *Aegiphila trifida*	No	–	–	–	–	–	–	–	–	+	+
Ardisia brittonii	Me	–	–	–	–	–	–	–	–	+	+
Calophyllum calaba	Me	–	–	–	–	–	–	–	–	+	–
Calyptronoma occidentalis	Me	–	–	–	–	–	–	–	–	+	+
Clidemia plumosa	Me	–	–	–	–	–	–	–	–	+	–
Cordia elliptica	Me	–	–	–	–	–	–	–	–	+	+
Drypetes alba	Mi	–	–	–	–	–	–	–	–	+	–
Eugenia spp. (2)	Mi	–	–	–	–	–	–	–	–	+	+
Picramnia antidesma	No	–	–	–	–	–	–	–	–	+	+
Piper discolor	No	–	–	–	–	–	–	–	–	–	+
Psychotria dolphiniana	Mi	–	–	–	–	–	–	–	–	+	–
P. cf. *glabrata*	No	–	–	–	–	–	–	–	–	–	+
Solanum acropterum	No	–	–	–	–	–	–	–	–	–	+
Symphonia globulifera	Mi	–	–	–	–	–	–	–	–	+	–
Tabernaemontana rendlei	No	–	–	–	–	–	–	–	–	+	–
Tetrorchidium rubrinervium	Me	–	–	–	–	–	–	–	–	+	–

* + = present; (+) = present but rare and not included in the determination of leaf-size spectrum; – = absent.

† According to the systems of Raunkiaer (1934) and Webb (1959). Le = leptophyll; Na = nanophyll; Mi = microphyll; No = notophyll; Me = mesophyll *sensu stricto*; Ma = macrophyll.

TABLE 3. Tree ferns, shrubs, herbs, and climbers present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains.*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Tree ferns											
Blechnum underwoodianum		+	−	−	−	−	−	−	−	−	−
Cyathea fragilis		+	−	−	−	−	−	−	−	−	−
C. furfuracea		−	+	+	+	?	−	−	−	−	−
C. hystricosa		−	+	+	+	?	−	−	−	−	−
C. pubescens		−	+	+	+	?	−	−	−	−	−
C. dissoluta		−	−	−	−	?	−	−	−	+	−
C. grevilleana		−	−	−	−	?	−	−	−	−	+
Cyathea sp.		−	−	−	−	−	+	−	−	−	−
Lophosoria quadripinnata		−	(+)	+	+	−	+	+	−	−	−
Shrubs and tall woody herbs											
Blakea trinervia	No	+	−	−	−	−	−	(−)	−	(−)	−
Miconia rigida	No	+	−	−	−	+	+	−	−	−	−
Lisianthius latifolius	No	−	+	+	+	−	−	−	−	−	−
Palicourea alpina	No	−	+	+	+	+	+	(+)	−	−	−
Psychotria corymbosa	Mi	−	+	+	+	+	+	(+)	−	−	−
Senecio cf. *fadyenii*	No	−	+	+	+	−	−	−	−	+	+
Wallenia laurifolia	No	−	+	+	+	+	+	(+)	−	−	−
Besleria lutea	Me	−	−	+	+	−	−	−	−	(+)	−
Cestrum hirtum	No	−	−	(+)	(+)	−	−	−	−	−	−
Boehmeria caudata	Me	−	−	−	+	−	−	−	−	−	−
Callicarpa ferruginea	Mi	−	−	−	+	−	−	−	−	+	−
Datura suaveolens	Me	−	−	−	(+)	−	−	−	−	−	−

TABLE 3. Tree ferns, shrubs, herbs, and climbers present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains (*continued*).*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Piper fadyenii or *P. hispidum*	No	–	–	–	(+)	–	–	–	–	–	–
Tournefortia glabra	Me	–	–	–	(+)	–	–	–	–	–	–
Cephaelis elata	Me	–	–	–	–	+	–	–	–	+	+
Lobelia martagon (WH‡)	No	–	–	–	–	–	+	–	–	–	–
Vernonia pluvialis	Mi	–	–	–	–	–	+	–	+	–	–
Baccharis scoparia	Le	–	–	–	–	–	(+)	+	–	–	–
Bidens shrevei	No	–	–	–	–	–	+	+	+	–	–
Bocconia frutescens (WH‡)	Ma	–	–	–	–	–	+	+	–	–	–
Eupatorium parviflorum	No	–	–	–	–	–	+	+	–	–	–
E. triste	Mi	–	–	–	–	–	–	+	+	–	–
Satureja viminea	Le	–	–	–	–	–	–	+	+	–	–
Vernonia divaricata	Mi	–	–	–	–	–	–	+	–	–	–
Salvia jamaicensis	Mi	–	–	–	–	–	–	–	+	–	–
Verbesina nervosa	No	–	–	–	–	–	–	–	+	–	–
Mecranium virgatum	No	–	–	–	–	–	–	–	–	+	–
Neea nigricans	No	–	–	–	–	–	–	–	–	+	–
Psychotria foetida	Me	–	–	–	–	–	–	–	–	+	–
P. uliginosa	Me	–	–	–	–	–	–	–	–	+	–
Wallenia subverticillata	No	–	–	–	–	–	–	–	–	+	–
Conostegia pyxidata	Mi	–	–	–	–	–	–	–	–	–	+
Gesneria calycina	No	–	–	–	–	–	–	–	–	–	+
Herbs											
Elaphoglossum latifolium		+	+	+	–	(–)	–	–	–	–	–
Gleichenia bancroftii		+	+	+	–	(+)	–	–	–	–	–
Liparis neuroglossa		(+)	(+)	(+)?	–	–	–	–	–	–	–
Peperomia cf. *clusiifolia*		+	(–)	–	–	–	–	–	–	–	–
Polystichopsis denticulata		+	–	–	–	–	–	–	–	–	–
Polypodium loreum		+	+	+	+	+	–	–	–	–	–
Trichomanes robustum		+	+	+	–	+	–	–	–	–	–
Blechnum striatum		–	+	+	–	+	–	–	–	–	–
Calanthe mexicana		–	(+)	(+)	–	–	–	–	–	–	–
Erythrodes plantaginea		–	+	(+)	+	?	–	–	–	+	–
Gesneria mimuloides		–	–	(+)	–	–	–	–	–	–	–
Liabum umbellatum		–	+	+	–	–	–	–	–	–	–
Liparis harrisii		–	(+)	(+)	–	–	–	–	–	–	–
Lycopodium taxifolium		–	(+)	–	–	–	–	–	–	–	–
Pilea weddellii		–	(+)	(+)	(+)	(+)	–	–	–	–	–
Peperomia alpina		–	+	+	+	–	(+)	–	–	–	–
Prescottia stachyodes		–	+	+	+	?	–	–	–	+	–
Rhynchospora polyphylla		–	+	+	+	–	–	–	–	–	–
Zeugites americana		–	+	+	+	(+)	+	–	–	–	–
Diplazium brunneo-viride		–	–	–	+	–	–	–	–	–	–
D. centripetale		–	–	–	+	–	–	–	–	–	–
Marattia alata		–	–	–	(+)	–	–	–	–	–	–
Pilea cf. *grandiflora*		–	–	–	+	–	–	–	–	–	–
Polypodium lanceolatum		–	–	–	(+)	–	–	–	–	–	–
Ponthieva harrisii		–	–	–	+	–	–	–	–	–	–
Selaginella denudata		–	–	–	–	+	–	–	–	+	+
Pteridium aquilinum		–	–	–	–	–	+	+	–	–	–
Rhynchospora eggersiana		–	–	–	–	–	+	–	–	–	–
Psychotria discolor		–	–	–	–	–	–	–	–	+	+
Thelypteris deltoidea		–	–	–	–	–	–	–	–	+	–

TABLE 3. **Tree ferns, shrubs, herbs, and climbers present in various forest types in the Blue Mountains, Port Royal Mountains, and John Crow Mountains** (*continued*).*

SPECIES	LEAF-SIZE CLASS †	MOR RIDGE FOREST	MULL RIDGE FOREST	WET SLOPE FOREST	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
Diplazium costale		–	–	–	–	–	–	–	–	–	+
Pilea sp.		–	–	–	–	–	–	–	–	–	+
Climbers and scramblers											
Anthurium scandens		+	+	+	+	+	–	–	–	–	–
Odontosoria jenmanii		(+)	+	+	+	+	–	–	–	–	–
Schradera involucrata		(+)	+	+	+	+	–	–	–	+	–
Smilax balbisiana		+	+	+	+	+	–	–	–	–	–
Cassia viminea		–	+	+	+	–	–	+	–	–	–
Chusquea abietifolia		–	+	+	+	+	+	+	+	–	–
Manettia lygistum		–	(+)	–	–	–	+	+	–	–	–
Marcgravia brownei		–	–	–	+	–	–	–	–	+	+
Cionosicys pomiformis		–	–	–	–	–	–	+	–	–	–
Cynanchum harrisii		–	–	–	–	–	–	+	–	–	–
Anthurium cordifolium		–	–	–	–	–	–	–	–	+	–
Lomariopsis underwoodii		–	–	–	–	–	–	–	–	+	–
Solandra sp.		–	–	–	–	–	–	–	–	+	–
Syngonium auritum		–	–	–	–	–	–	–	–	+	+

* + = present; (+) = present but rare; – = absent; (–) = present only as an epiphyte.

† Listed for the shrubs; according to the systems of Raunkiaer (1934) and Webb (1959). Le = leptophyll; Na = nanophyll; Mi = microphyll; No = notophyll; Me = mesophyll *sensu stricto*; Ma = macrophyll.

‡ WH = woody herb.

glauca, *Dilomilis montana* (Sw.) Summerh. (= *Octadesmia montana* (Sw.) Bentham), *Pleurothallis oblongifolia*, *Stelis micrantha*, and *S. trigoniflora* (Sw.) Garay & Sweet (= *S. ophioglossoides* (Jacq.) Sw.). Hummocks of the moss *Leucobryum giganteum* C.M. 5 to 20 cm. across are frequent. However, *Sphagnum* is absent from MOR RIDGE forest in the Morce's Gap area. In the Blue Mountains and Port Royal Mountains *Sphagnum* is generally a weed of paths, but it was seen once in apparently undisturbed MOR RIDGE forest — on Silver Hill Peak about 1 km. west of John Crow Peak (obs. E. V. J. T.).

Climbers and scramblers are uncommon and all thin-stemmed. Only four species are found (TABLE 3), and of these *Anthurium scandens* is by far the commonest, creeping on the forest floor as often as up the trunks. The bamboo *Chusquea abietifolia* is absent.

Vascular epiphytes are very frequent. Bromeliads are particularly prominent (mostly *Tillandsia complanata* and *Vriesia sintenisii*, with some *Vriesia incurva* and a single plant of *Guzmania fawcettii*). Orchids are also very common (the five species listed above plus *Epidendrum ramosum*, *E. repens*, *Jacquiniella teretifolia*, and *Lepanthes ovalis*). So are the ferns, the most abundant (*Hymenophyllum polyanthos* and *H. sericeum*) being filmy and the others (*Grammitis curvata* (Sw.) Ching, *G. graminea*, and *G. trichomanoides*) mostly small-fronded. *Polypodium loreum* is occasionally epiphytic, *Lycopodium taxifolium* is rare, and *Columnea hirsuta* is occasional. Epiphytic bryophytes are common, but the degree of "mossing" is not very marked; the bryophyte cover on the trunks is never more than 50 per cent and usually less than 20 per cent. Epiphylls are rare. The lichen *Usnea* is common in the crowns.

Hemiparasites were not obvious from the ground, but when trees were felled for biomass estimation, they were found to be frequent, apparently especially on *Lyonia*. The species involved were *Dendropemon parvifolius*, *Dendrophthora opuntioides* (by far the commonest), and *Eubrachion ambiguum*. No parasitic or saprophytic vascular plants were seen in the herb layer.

There are no buttresses on the trees, no cauliflorous species, and no leaves with drip-tips. Compound leaves are seen only on *Schefflera* and the tree ferns. The leaf-size spectrum of the trees and shrubs (excluding the tree ferns and the three species represented by only one mature individual each) is shown in TABLE 4; microphylls and notophylls are most abundant. As in many other low-stature forests on tropical mountains, the leaves of the trees and shrubs are mostly thick and more or less coriaceous (cf. Howard, 1968; Grubb, 1974).

Fully developed MOR RIDGE forest has been found by one of us (E. V. J. T.) on several knolls along the ridge from Morce's Gap over John Crow Peak to Silver Hill Peak. In addition, many sites along this ridge show stages in the development of mor.

MULL RIDGE and WET SLOPE forests. These two forest types are very similar and are treated together here. They differ from the MOR RIDGE

TABLE 4. Percentages of tree and shrub species in the various forest types in the leaf-size classes of Raunkiaer (1934) modified by Webb (1959).

	MOR RIDGE FOREST	MULL RIDGE AND WET SLOPE FORESTS	GULLY FOREST	VERY WET RIDGE FOREST	HIGH ALTITUDE FOREST	DRY SLOPE FOREST	DRY LIMESTONE SCRUB FOREST	WET LIMESTONE FOREST (LOWER)	WET LIMESTONE FOREST (UPPER)
LEPTOPHYLL	—	—	—	—	—	11	8	—	—
NANOPHYLL	13	2	3	11	14	—	15	—	—
MICROPHYLL	40	46	41	32	33	43	54	25	16
NOTOPHYLL	40	44	47	53	38	39	23	40	60
MESOPHYLL *sensu stricto*	7	7	9	5	5	4	—	35	24
MACROPHYLL	—	—	—	—	10	4	—	—	—
MEGAPHYLL	—	—	—	—	—	—	—	—	—

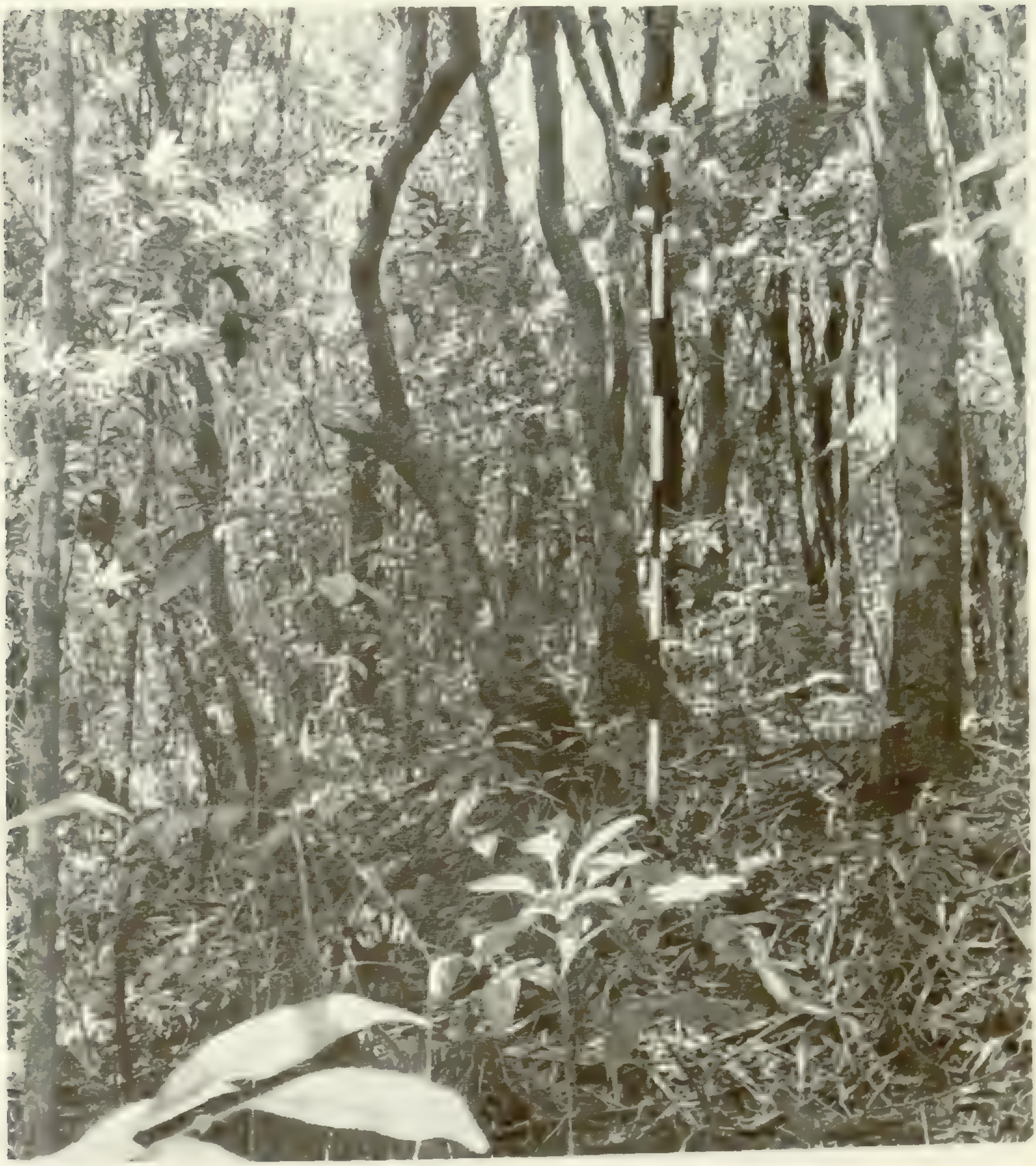

FIGURE 4. **Mull Ridge forest.** Scale pole marked in feet. Saplings of *Dendropanax pendulus* in center foreground; *Podocarpus urbanii* on left; *Cyathea furfuracea* in right background. February, 1975. Photo by E. V. J. Tanner.

forest type in being taller (8 to 13 meters), in having a closed canopy, and in having many fewer epiphytes, both vascular and nonvascular. The trees in the SLOPE forest are generally taller and frequently lean downhill. On the ridge tops there are occasional trees of larger girth (*Cyrilla racemiflora* to more than 70 cm. DBH, *Lyonia* cf. *jamaicensis* to more than 45 cm. DBH, and *Podocarpus urbanii* Pilger to more than 50 cm. DBH); such trees also occur less frequently on the slopes. The MULL RIDGE forest is notably easier to walk through than the MOR RIDGE forest because of the general lack of leaning trees and the greater height to the first branch on most trees. There are a much larger number of dicotyledonous tree species present — 47 were recorded, although of

FIGURE 5. **Wet Slope forest.** Scale pole marked in feet. Trunk arching over pole is of *Cyrilla racemiflora*. Upright trunk on left is of *Clethra occidentalis*; trunk with protuberances at top right is of *Hedyosmum arborescens*. Tree fern in foreground is *Cyathea pubescens* (always short-stemmed on slope). February, 1975. Photo by E. V. J. Tanner.

these 12 were represented by only very few individuals (TABLE 2). Several of the trees absent from the MOR RIDGE forest (TABLE 2) are frequent in the MULL RIDGE and WET SLOPE forests, e.g. *Calyptranthes rigida*, *Dendropanax "pendulus,"*[5] *Eugenia* spp., and *Hedyosmum arborescens*. Tree ferns are much more numerous, taller, and attain greater girths; the species are quite different (TABLE 3).

There is a well-developed though discontinuous shrub layer about 2 to 3 meters tall, containing seven species (TABLE 3) but composed chiefly

[5] Possibly including some *D. nutans*.

of *Palicourea alpina* and *Psychotria corymbosa* (both Rubiaceae). Herbs are present in greater variety than in the MOR RIDGE forest; most of the species present in the latter forest occur, in addition to quite a number of others (TABLE 3). The most frequent are the terrestrial orchids (*Erythrodes plantaginea* and *Prescottia stachyodes*). The hummock moss *Leucobryum* is decidedly less common than in the MOR RIDGE forest.

The climbers and scramblers are few in number (TABLE 3), and all are thin-stemmed. The bamboo *Chusquea abietifolia* is only occasional, but it forms localized, impenetrable thickets. The vascular epiphytic species are much as in the MOR RIDGE forest, although *Columnea hirsuta* is generally absent, while the bromeliad *Hohenbergia fawcettii* is present but rare. In addition, *Peperomia* cf. *clusiifolia* occurs here occasionally as an epiphyte. No critical observations were made on the hemiparasites; *Phoradendron flavens* was seen in the MULL RIDGE forest on the ascent of Blue Mountain Peak but not in the Morce's Gap area.

As in the MOR RIDGE forest, the trees have no buttresses and there are no cauliflorous species. Only two species represented by more than a very few individuals have drip-tips (*Dendropanax "pendulus"* and *Eugenia virgultosa*), and only two have compound leaves (*Guarea swartzii* and *Schefflera sciadophyllum*). The leaf-size spectrum of the trees and shrubs (excluding the tree ferns and the species represented by very few individuals) is similar to that in the MOR RIDGE forest (TABLE 4). However, the average leaf texture is decidedly less coriaceous.

The MULL RIDGE — WET SLOPE forest is certainly worthy of recognition as a separate association from the MOR RIDGE forest, since it contains many more species, including trees, shrubs, and herbs. We agree with Asprey and Robbins (1953) that this forest type (their "MONTANE MIST" forest) appears to be rather uniform floristically over wide areas, but we cannot agree with their statement (1953, p. 400) that "the dominants are *Podocarpus urbanii* and *Cyrilla racemiflora*." Dominance, in fact, seems to be shared by three, four, or five species at any one site, and it is perhaps unfortunate that Asprey and Robbins called this forest type the "*Podocarpus-Cyrilla* association."

GULLY forest. Our impression of this forest type in the Cinchona-Morce's Gap–John Crow Peak area and the Portland Gap–Blue Mountain Peak area agrees closely with the description given by Shreve. The GULLY forest differs from those so far considered in its greater height (12 to 18 meters), much taller boles, and fairly frequent buttresses (0.8 meters high), as well as in the presence of the woody liana *Marcgravia brownei*, which develops stems 3 cm. thick and climbs high into the canopy. The mean girth of the trees is certainly greater than on the slopes and ridges, but it seems that few trees (mostly *Solanum punctulatum*) exceed 40 cm. DBH. Twenty-six dicotyledonous tree species and four species of tree fern were recorded, all of them represented by many individuals. Floristically the forest is quite distinct from that on slopes and ridges, despite the occurrence of the six "core" species and many

FIGURE 6. **Gap forest (uppermost end of Gully forest).** Scale pole marked in feet. Tree on right with buttresses is *Clethra occidentalis*; seedling in front of it is *Eugenia virgultosa*. All tree ferns are *Cyathea pubescens*. February, 1975. Photo by E. V. J. Tanner.

of the species of MULL RIDGE — WET SLOPE forest (cf. TABLES 2 and 3). All of the MOR RIDGE species of trees (TABLE 2) are absent, while there are five species decidedly more common in gullies than on slopes and ridges and quite absent from mor sites. Of these latter species, three (*Laplacea haematoxylon*, *Solanum punctulatum*, and *Turpinia occidentalis*) are able to grow 15 to 18 meters tall, and these contribute significantly to the structure of the forest, especially the *Solanum*.

The shrub layer is similar to that in the MULL RIDGE — WET SLOPE forest but includes much more *Besleria lutea* and one additional frequent species, *Boehmeria caudata*. Isolated individuals of four more species

were seen (cf. TABLE 3); two of them, *Datura suaveolens* and *Tournefortia glabra*, are more often seen in the mountains as weeds (C. D. Adams, pers. comm.). Compared with the shrub layer, the herb layer contains relatively more species absent from the MULL RIDGE — WET SLOPE forest and lacks more species widespread in the latter forest type (cf. TABLE 3).

The climbers are much as in the MULL RIDGE — WET SLOPE forest (with the addition of *Marcgravia brownei*). The same appeared to be true of the vascular epiphytes in the sites which we studied, although it appears from Shreve's account (pp. 38–41) that there are several additional species on the lower parts of the boles in many windward ravines. Certainly the growth of epiphytic bryophytes is appreciably greater in the more sheltered gullies.

The forest resembles the forests on slopes and ridges in its lack of cauliflory and paucity of species with compound leaves or drip-tips. The leaf-size spectrum shows a somewhat greater development of notophylls relative to microphylls (TABLE 4).

VERY WET RIDGE forest. Structurally and floristically this forest on Mt. Horeb is very like the MULL RIDGE — WET SLOPE forest of the Blue Mountains. The floristic resemblance is shown for the trees in TABLE 2 and for the shrubs, herbs, and climbers in TABLE 3. The forest differs in the greater abundance of epiphytic bryophytes (the cover on trunks is generally 50 per cent and may add 20 per cent to the apparent DBH) and in the abundance of the small-fronded *Selaginella denudata* on the forest floor. It also differs in the abundance of large bromeliads on the bigger, older trees. The commoner species of the Morce's Gap area (*Tillandsia complanata* and *Vriesia sintenisii*) are present, but the species less common there (*Hohenbergia fawcettii* and *Vriesia incurva*) were not seen on Mt. Horeb. The most abundant (and also the largest) species on Mt. Horeb (*Guzmania fawcettii*) was found only once near Morce's Gap. A further indicator of wetness is the presence of the shrub *Cephaelis elata*, common in the WET LIMESTONE forest and typical of "sheltered *facies* of montane woodland" according to Adams (1972).

This forest would perhaps best be classified as a distinct *facies* of the MULL RIDGE — WET SLOPE association.

HIGH ALTITUDE forest. This was visited only once, and our account is therefore less reliable than that for the other forest types. It is generally 3 to 6 meters tall, but reduced to 1.5 to 2.0 meters toward the summit of Blue Mountain (over 2000 meters). The trees are generally upright. On a few north-facing cliffs and on certain ridges we noticed severe wind-pruning of trees and shrubs, at least some of which had smaller and thicker leaves than usual.[6] However, most of the dwarfed forest, including that near the summit, shows no sign of wind-pruning. Twenty-

[6] The same was seen at a lower altitude (1670 meters) in Portland Gap.

three species of trees were recorded, including two tree ferns; nine were recorded as very rare, mostly found near the lower limit of the forest type. The species present are an interesting mixture (TABLE 2). Of the six "core" species of lower altitudes only three are present; of the ten ridge and slope species of lower altitudes only two are present other than as rare isolated individuals; and of the 23 ridge, slope, and gully species only one occurs. Of the five gully species only one is present. The three tree species confined to the HIGH ALTITUDE forest all have leaves which represent types characteristic of SUBALPINE forest on the high equatorial mountains: close-packed glabrous nanophylls in *Eugenia alpina*, densely hairy mesophylls in *Clethra alexandri*, and densely hairy macrophylls in *Senecio swartzianus*.

It is interesting that several DRY SLOPE forest species are found in the HIGH ALTITUDE forest, some of them (*Garrya fadyenii*, *Viburnum alpinum*, and *V. villosum*) repeatedly and others (*Brunellia comocladiifolia*, *Miconia quadrangularis*, *Myrica cerifera*, *Rhamnus sphaerospermus*, and *Weinmannia pinnata*) only as isolated individuals. Adams (1972) also records that *Myrsine coriacea* ascends as far as the top of Blue Mountain. All of these species occur in spite of the undoubted fact that the HIGH ALTITUDE forest is fogged for much longer periods than the MULL RIDGE forest of lower altitudes, where they do not normally occur. The high altitude slopes concerned have undoubtedly been disturbed to some extent as a result of their proximity to the long-used track to Blue Mountain Peak, but it seems most unlikely that the DRY SLOPE forest species have gained entrance to the community purely as a result of disturbance.

The shrubs show a similar pattern of development, with few of the species of moist forests at lower altitudes present (TABLE 3) and at least four of the species which are found in DRY SLOPE forest or DRY LIMESTONE scrub forest at lower altitudes. The one apparently obligate HIGH ALTITUDE "shrub" (really a woody herb), *Lobelia martagon*, again represents a life form characteristic of the Subalpine Zone on equatorial mountains. However, it should be noted that it is sometimes found below 1850 meters, even as low as 750 meters on occasion (Adams, 1972). *Lobelia alticaulis*, similarly woody but virtually unbranched, is found in the John Crow Mountains at 600 to 750 meters (Adams, 1972).

The HIGH ALTITUDE forest is deficient in tree ferns (no material of those present was collected), herbs, and climbers (TABLE 3). *Chusquea* and bracken (*Pteridium aquilinum*) are occasional, and a large-fronded species of *Gleichenia* (not collected) is locally abundant. Vascular epiphytes and hemiparasites are very few. "Mossing" is about the same as in the MULL RIDGE forest or less marked, except on certain north-facing slopes, where it is very obvious.

The leaf-size spectrum of the trees and shrubs (other than tree ferns and very rare species) shows a very wide spread (TABLE 4). Only two species, *Schefflera sciadophyllum* and *Weinmannia pinnata* (both very rare), have compound leaves, although two others, *Bocconia frutescens* and *Senecio swartzianus*, have deeply dissected leaves. Only one species,

Dendropanax "*nutans*",[7] has drip-tips. There are no buttressed or cauliflorous species. The HIGH ALTITUDE forest clearly represents a distinct association.

The vegetation around the summit of Blue Mountain has been very severely disturbed. However, about 100 meters to the east, on a flat area of 1 to 2 hectares, there is a distinct *facies* of the HIGH ALTITUDE forest which does not appear to have suffered much human interference, unless it was by fire at some time in the distant past. *Clethra alexandri* (2(to 2.5) meters tall) is the most abundant tree, followed by *Eugenia alpina*, then *Dendropanax "nutans"*, *Ilex macfadyenii*, *Vaccinium meridionale*, and *Viburnum alpinum* or *villosum* (all of which are occasional), and finally *Podocarpus urbanii* and *Cyathea* sp. (both rare). There are two occasional shrubs, *Eupatorium parviflorum* and *Wallenia* sp. The tall woody herb *Lobelia martagon* is frequent and contributes significantly to the physiognomy of the community. In the herb layer *Rhynchospora eggersiana* is frequent, *Blechnum* sp. and *Lophosoria quadripinnata* are occasional (the latter with fronds dwarfed to less than 1 meter in length instead of the usual 1.5 to 2.0 meters), and *Lycopodium clavatum* is locally abundant. The soil appears to be more or less evenly and markedly enriched with organic matter (though not "peaty") to a depth of 30 cm., where stones are encountered. The surface pH is 4.3–4.5 and that at a depth of 30 cm. is 4.3 (two samples).

DRY SLOPE forest. This community, as mentioned earlier, has been almost totally destroyed by man. Its lower limit is now quite obscure, but the community seems to have stretched down to about 1000 to 1100 meters at least; the upper limit is about 1500 meters. The least disturbed remnants are 6 to 11 meters tall; most of the trees are upright and few attain a DBH of 40 cm.

Many of the most disturbed areas are now dominated by shrubs and low trees, some of which are markedly xeromorphic, in particular the switch plant *Baccharis scoparia*, the tiny-leaved *Satureja viminea*, and the sticky-leaved *Dodonaea viscosa*. Soft-leaved Compositae (*Bidens*, *Eupatorium*, and *Vernonia*) are locally prominent.

The forest and associated scrub contain 26 species of dicotyledonous trees, one tree fern, and ten shrubs. Of these, 13 trees and seven shrubs constitute a distinct suite, more common here than in any other forest type studied (TABLES 2 and 3). It is notable that fewer than half of the hard-leaved tree species of the ridges and wet slopes are present on the dry slopes. Of the species that are present (e.g., *Ilex obcordata*, *Podocarpus urbanii*, and *Vaccinium meridionale*), none are particularly common. It is, therefore, unfortunate that Asprey and Robbins called the community "Montane Sclerophyll." It is markedly less "sclerophyllous" than the MOR RIDGE forest and somewhat less "sclerophyllous" than the MULL RIDGE forest.

Tree ferns, apart from *Lophosoria quadripinnata* (which has only a

[7] Possibly including some *D. pendulus*.

short trunk), appear to be quite absent from the DRY SLOPE forest at the present time. We were told, however, that tall tree ferns with copious development of adventitious roots on the trunks had been cut out from the wettest parts of the DRY SLOPE forest along the path from Cinchona to Morce's Gap for sale to orchid-growers.

The herb layer was not studied in detail. It is extremely difficult now to determine what the original herbaceous species were because of the great influx of weeds. There are few climbers (TABLE 3) and relatively few epiphytes.

There are no cauliflorous or buttressed species; only one species (*Brunellia comocladiifolia*) has compound leaves and none have drip-tips. The leaf-size spectrum of the trees and shrubs (excluding the tree fern and very rare species) shows the widest spread of all the forest types studied by us, but the two most abundant leaf-size classes are as in the MULL RIDGE — WET SLOPE forest, i.e., microphylls and notophylls (TABLE 4). The forest clearly represents a further distinct association.

DRY LIMESTONE scrub forest. On the southeast side of John Crow Peak at 1750 to 1800 meters, growing amongst the deeply dissected limestone, is a distinctive scrub forest 2 to 4 meters tall, with most stems only 2 to 3 cm. thick at 1 meter in height (a few are 6 cm. thick). This community is remarkable for the almost complete absence of the more or less hard-leaved tree species of the RIDGE and SLOPE forests (TABLE 2). Apart from abundant *Chusquea abietifolia* (which covers about 75 per cent), the dominant shrub species are the soft-leaved *Eupatorium triste* and *Vernonia pluvialis*, the leptophyllous *Satureja viminea*, and the more or less succulent-leaved *Verbesina nervosa*. The soft-leaved *Salvia jamaicensis* is also characteristic, and the scrambling shrub *Bidens shrevei* (also soft-leaved) is present. The leaf-size spectrum shows a predominance of microphylls (TABLE 4), and in this sense the community is relatively xeromorphic. However, the leaf texture is mesomorphic (as is indeed the leaf texture of the dominant species on limestone in the lowlands in the dry southwestern part of Jamaica). The change from the hard-textured leaves of the MOR RIDGE forest to the soft-textured leaves of the LIMESTONE scrub forest in many ways parallels the change from bog to fen vegetation in northern Europe. One might expect the soft-leaved species of the LIMESTONE scrub forest to be at least facultatively deciduous. However, they were found not to have lost their leaves toward the end of the main dry season (in March) in 1974 (obs. E. V. J. T.). Of the few harder-leaved species present, the most interesting perhaps is *Weinmannia pinnata*, otherwise seen by us only in HIGH ALTITUDE forest, on Mt. Horeb, and in the John Crow Mountains, but described by Adams (1972) as "locally frequent in montane thickets and open woodlands, 3600–6500 ft."

Down in the grykes between the rugged blocks of limestone there is virtually no herb layer, although in solution hollows on the tops of the rocks a few herbaceous species are found (*Peperomia quadrifolia*, *Pilea microphylla*, *Relbunium hypocarpium*, and a few orchids and bromeliads).

Bryophytes are absent from the trunks of most of the shrubs, but the lichen *Usnea* is very frequent on emergent crowns. The hemiparasite *Eubrachion ambiguum* was noted.

WET LIMESTONE forest. On the summit of John Crow Peak in the Blue Mountains, the vegetation is quite different from that just described. The ground is not deeply dissected, although there are outcropping rocks of limestone. The vegetation is, in general appearance, like that of the MULL RIDGE forest, but we did not have an opportunity to study it critically.

The WET LIMESTONE forest was studied in some detail on the western slopes of the John Crow Mountains. Here there appeared to be a continuum, at the lower end of which the forest was 15 to 18 meters tall, with frequent buttresses more than 1 meter high and occasional prop roots, and at the upper end of which the forest was 8 to 11 meters tall without buttresses or prop roots. Two sites were chosen for detailed study (at 770 meters and 950 meters) to represent the extremes. Throughout the continuum the canopy is closed, the trees are upright, and there is no evidence of wind-clipping. At the lower end many trees with a DBH greater than 40 cm. are present, but at the upper end the forest is denser and there are few individuals with a DBH greater than 15 cm. The forest differs from all of those described so far in the presence of a species of palm, *Calyptronoma occidentalis*, which is generally frequent at the lower end of the continuum but more or less confined to gullies at the upper end.

Twenty-three species of angiospermous trees, one tree fern, and 11 species of shrubs were recorded at the lower site, of which only 12 angiospermous trees and one shrub were present at the upper site. Ten angiospermous trees, one tree fern, and two shrubs were recorded at the upper site and not at the lower. Although the list of herbs in TABLE 3 is certainly less complete than that for the other forest types, the herb layer is undoubtedly poor in species. This is especially true at the upper end of the continuum, where the herb layer is occupied almost exclusively (apart from tree seedlings) by the fern *Diplazium costale*, with upright stems 10 to 15 cm. tall.

Climbers are abundant at the lower end of the continuum and, though fewer species are present, they are still frequent at the upper end. *Syngonium auritum* (Araceae), which climbs to the lower part of the canopy, is particularly prominent throughout.

Vascular and nonvascular epiphytes throughout are approximately as abundant as in the MULL RIDGE forest of the Blue Mountains. The following vascular epiphytes were collected: *Catopsis nitida*, *Guzmania fawcettii*, and *Hohenbergia eriostachya* (all bromeliads); *Arpophyllum jamaicense*, *Epidendrum polybolbon*, *Maxillaria purpurea*, *Neourbania adendrobium*, and *Pleurothallis uncinata* (all orchids); *Polytaenium fcei* (fern); *Blakea trinervia* (melastome); and *Columnea fawcettii* (gesneriad). Although our collections are again bound to be incomplete, it is notable that

the bromeliad and orchid species involved are all different from those recorded in the Blue Mountains *sensu stricto* except the *Guzmania*, which is very rare in the latter range. The *Pleurothallis*, like the *Guzmania*, is found on Mt. Horeb, and the *Arpophyllum* occurs at Newcastle nearby (C. D. Adams, pers. comm.).

No cauliflorous species were found, only two species with compound leaves (*Calyptronoma occidentalis* and *Guarea swartzii*), and only one with drip-tips (*Psychotria dolphiniana*). The leaf-size spectrum of the trees and shrubs (other than tree ferns and very rare species) shows a clear preponderance of notophylls and mesophylls *sensu stricto*.

No detailed study was made of the community above 950 meters, where there was a steep, dissected slope with grykes 0.5–2.5 meters across and large blocks of limestone completely devoid of soil. The whole slope was covered by a low forest with a closed canopy, the very tortuous trunks and roots running over the rocks. Bryophytes are very abundant through the canopy and over the trunks, roots, and rocks. The trees present in the lowermost part of this community include *Guarea swartzii* and *Piper discolor* (also found in the continuous forest below) and *Conostegia icosandra*, *Viburnum alpinum*, and *Wallenia venosa*. Also found were the shrub *Gyrotaenia microcarpa*, the herbs *Lobelia grandiflora*, *Pilea grandiflora*, and *Psychotria discolor*, and the epiphyte *Elaphoglossum crinitum*. This community above 950 meters is termed "Elfin Woodland" by Asprey and Robbins (1953), who recorded *Clusia havetioides* (as *C. clarendonensis*) as the most abundant species. C. D. Adams and G. R. Proctor (pers. comm.) agree that this species is abundant over wide areas on the eastern (dip) slope of the mountains. *Clusia portlandiana* is also present, indeed confined to the John Crow Mountains, but it is not known whether it is a widespread and abundant species (C. D. Adams, pers. comm.).

It is notable that 15 of the tree species and two of the shrub species present in the WET LIMESTONE forest are also found in the MULL RIDGE — WET SLOPE forest of the Blue Mountains and/or the VERY WET RIDGE forest of Mt. Horeb; one more is known in the DRY SLOPE forest of the Blue Mountains (TABLES 2 and 3). Of the remaining 13 trees and seven shrubs in the WET LIMESTONE forest identified with certainty to species level, only nine trees and four shrubs are recorded by Adams (1972) as generally occurring on limestone. Most of these 13 apparently calcicolous species are rare or absent above 900 meters. Whether they are strictly calcicolous is doubtful, because relatively little rain forest remains in the appropriate altitudinal range on soils derived from rocks other than limestone, and such sites have not been studied critically. A high proportion of the species in the community above 950 meters are certainly found elsewhere off limestone, i.e. all of the 12 recorded by Asprey and Robbins (1953, p. 402) except *Conostegia balbisiana* and *Garcinia humilis* ("*Rheedia sessiliflora*")[8] and all of the ten recorded by us other

[8] *Clusia 'clarendonensis'* is excepted, since this was a misidentification of *C. havetioides*.

than *Conostegia icosandra*, *Lobelia grandiflora*, *Psychotria discolor*, and *Wallenia venosa*.

RESULTS OF FOLIAR ANALYSES

In December, 1973, mature, well-lit leaves were collected from the crowns of two individuals of almost all the major tree species in a stretch of MOR RIDGE forest on one of the knolls west of Morce's Gap. The leaves were oven-dried within two days of collection. In late July to early August, 1974, mature, well-lit leaves were collected from the crowns of three individuals of each of two "core" species (*Alchornea latifolia* and *Clethra occidentalis*) in the MOR RIDGE, MULL RIDGE, WET SLOPE, and GULLY forests in the same area west of Morce's Gap. The gully forest in which we collected grew in a slight dip in the ridge and represents the uppermost limit of what we have described as GULLY forest. The leaves were oven-dried within one day of collection. Leaves from both collections were analyzed by standard methods (cf. Tanner, in press).

The results are set out in TABLES 5 and 6. The interpretation of foliar analyses always presents problems, and these are discussed elsewhere (Grubb, in prep.). The level of N, on a dry-weight basis, is largely a measure of leaf structure, since it is lower in leaves with a coriaceous texture, which reflects the development of thick cell walls, especially in the epidermides and bundle sheaths. This is less completely true of P or K, and leaf cell-wall thickness is not generally the major determinant of the levels of other mineral elements. These generalizations seem to hold for the present results. Thus, on the whole, the lowest N levels are found in the species with the most coriaceous leaves and, almost certainly, the thickest walls, i.e. *Ilex obcordata*,* *Clusia havetioides*,* *Podocarpus urbanii*, *Ilex macfadyenii*, *Chaetocarpus globosus*,* and *Lyonia* cf. *octandra*.* Of these species, the four marked with asterisks all attain their greatest abundance in the MOR RIDGE forest and contribute very largely to the impression of a particularly coriaceous leafy canopy in this forest type. The six species with the lowest P levels include five of the six species named above (all except the *Lyonia*), and the six species with lowest K levels include four of the six named above (not the *Chaetocarpus* or the *Clusia*).

If we consider, by way of contrast, the five species that not only grow in the MOR RIDGE forest but also appear to be about equally frequent in the GULLY forest (*Alchornea latifolia*, *Clethra occidentalis*, *Cyrilla racemiflora*, *Mecranium purpurascens*, and *Podocarpus urbanii*), we find that three of these (the *Alchornea*, *Clethra*, and *Mecranium* species) show the highest levels of N and P and two of the highest levels of K.[9] These results suggest that the coriaceous-leaved species of the MOR RIDGE for-

[9] *Blakea trinervia*, which is commonly an epiphyte and only found as a ground-dwelling species in the Morce's Gap area in the MOR RIDGE forest, has notably high levels of N, P, and K; these are consistent with the somewhat succulent nature of the leaves and, therefore, the ratio of protoplast to wall material.

TABLE 5. **The average foliar concentrations of various mineral elements in mature leaves collected in December, 1973, from Mor Ridge forest west of Morce's Gap.***

	N	P	K	Na	Mg	Ca	Mn	Fe	Zn	Cu
Aquifoliaceae										
Ilex macfadyenii	0.97	0.038	0.27	0.13	0.21	0.58	0.015	74	33	3.2
I. obcordata	0.72	0.028	0.22	0.31	0.18	0.44	0.011	96	22	4.2
Clethraceae										
Clethra occidentalis	1.27	0.051	0.42	0.08	0.71	1.47	0.047	93	41	4.1
Cyrillaceae										
Cyrilla racemiflora	1.14	0.045	0.37	0.25	0.15	0.20	0.005	74	19	2.0
Ericaceae										
Lyonia cf. *octandra*	1.06	0.047	0.32	0.05	0.15	1.05	0.024	93	61	7.7
Vaccinium meridionale	1.19	0.040	0.34	0.07	0.15	0.31	0.011	56	12	3.2
Euphorbiaceae										
Alchornea latifolia	1.57	0.100	0.46	0.03	0.21	0.94	0.017	107	24	5.7
Chaetocarpus globosus	1.00	0.041	0.38	0.04	0.16	0.22	0.009	89	25	3.5
Guttiferae										
Clusia havetioides	0.76	0.040	0.41	0.21	0.29	0.92	0.023	78	22	3.5
Melastomataceae										
Blakea trinervia	1.51	0.067	0.64	0.04	1.04	1.81	0.002	99	33	7.2
Mecranium purpurascens	1.49	0.053	0.33	0.18	0.55	0.34	0.003	78	14	3.5
Podocarpaceae										
Podocarpus urbanii	0.79	0.039	0.24	0.20	0.06	0.98	0.021	93	14	3.0

* Each value is the mean of two collections. Results are expressed as percentage dry weight for most elements, but as p.p.m. dry weight for Fe, Zn, and Cu.

est might be enabled to flourish there by an ability to withstand particularly low levels of N, P, and K supply, such as are commonly found in highly acid, highly organic soils in the temperate zones. The species concerned also tend to have the lowest foliar levels of Ca, Mg, and Mn, but the levels of these elements are not so consistently or markedly low.

The results in TABLE 6 for *Alchornea* and *Clethra* do not altogether confirm the above expectations. Certainly there is evidence from both species that the K supply is markedly worse in the MOR RIDGE forest soil than in the MULL RIDGE soil and notably better in the GULLY soil. However, only the results for *Alchornea* suggest any significant differences for N, and neither species yields any evidence of significant differences in P supply. The results for Ca and Mg are rather surprising, with the highest levels in both species being found at the MOR RIDGE and WET SLOPE sites. There are no consistent intersite differences in Mn, Fe, Cu, Zn, or Na. These results are considered later in relation to probable limiting factors.

DISCUSSION

THE FOREST FORMATIONS

We will now consider the classification of the Jamaican mountain forests in the scheme of formation types found useful in other parts of the wet tropics (summarized in TABLE 1) and tentatively relate the forests of the wetter parts of the lowlands to the same scheme.

The MOR RIDGE forest meets every criterion of the UPPER MONTANE rain forest in TABLE 1 except the predominance of microphylls (cf. TABLE 4). The same is true of the MULL RIDGE — WET SLOPE forest type, despite its greater stature and softer-textured leaves. The VERY WET RIDGE forest on Mt. Horeb is closely related to the latter type, separable merely as a *facies* in floristic terms, yet it shows a marked tendency toward a larger mean leaf size (TABLE 4). The HIGH ALTITUDE forest and DRY SLOPE forest are also clearly referable to the UPPER MONTANE rain forest formation type on all criteria except the leaf-size spectrum. All of these forests are notable for their lack of buttresses and thick-stemmed lianas. In contrast, the GULLY forest characteristically has these features, as well as significantly greater stature and a fairly clear preponderance of notophylls and mesophylls *sensu stricto*. Clearly, in the Jamaican situation, the leaf-size spectrum alone is not useful for the classification of MONTANE rain forests, but we consider that, taking all the positive features of the GULLY forest together, this association is best classified as an impoverished form of LOWER MONTANE rain forest. It is impoverished in the sense that it is of lower stature and contains fewer species (especially of woody climbers) than the LOWER MONTANE rain forests on most equatorial mountains (cf. Grubb *et al.*, 1963; Grubb & Stevens (in press); Whitmore, 1975). The fact that there is an appreciable overlap of tree species between the LOWER MONTANE and UPPER MONTANE forests in Jamaica emphasizes the importance of variations in plant per-

TABLE 6. The average foliar concentrations of various mineral elements in mature leaves collected in July and August, 1974, from four forest types west of Morce's Gap.

	N	P	K	Na	Mg	Ca	Mn	Fe	Zn	Cu
Alchornea latifolia										
MOR RIDGE	1.46	0.10	0.32	0.046	0.28	0.88	0.037	0.011	19	5.0
MULL RIDGE	1.59	0.09	0.59	0.034	0.16	0.64	0.039	0.010	19	4.1
WET SLOPE	1.64	0.11	0.68	0.036	0.24	0.75	0.012	0.011	6	1.4
GULLY	1.67	0.12	0.82	0.036	0.16	0.67	0.033	0.010	24	8.1
Clethra occidentalis										
MOR RIDGE	1.04	0.06	0.93	0.049	0.51	0.69	0.050	0.012	24	5.1
MULL RIDGE	1.07	0.06	1.25	0.033	0.26	0.47	0.031	0.010	22	4.3
WET SLOPE	1.27	0.08	1.38	0.054	0.49	0.73	0.033	0.012	22	5.8
GULLY	1.09	0.07	1.73	0.052	0.28	0.39	0.031	0.010	42	4.4

* Each value is the mean of three collections. Results are expressed as percentage dry weight for most elements, but as p.p.m. dry weight for Zn and Cu.

formance in the development of distinct forest formations. The same point is made by Grubb and Stevens (in press) for forest types in New Guinea.

The forest at the lower end of the continuum found on limestone in the John Crow Mountains is also clearly referable to LOWER MONTANE rain forest by every criterion in TABLE 1. The forest at the upper end of the continuum, however, is intermediate between LOWER MONTANE and UPPER MONTANE, having prominent climbers and a clear dominance of notophylls — mesophylls (typical of LOWER MONTANE forest), but low stature and an absence of buttresses (typical of UPPER MONTANE forest). We could not study the Limestone Pavement forest above 950 meters in any detail, but it is probably best assigned to the UPPER MONTANE rain forest formation. Asprey and Robbins included this forest type with our HIGH ALTITUDE forest in "Elfin Woodland," but since the communities are quite distinct in structure, physiognomy, and floristics, we do not find this treatment useful. As for our DRY LIMESTONE scrub forest, there is no widespread world vegetation type corresponding to it. It could possibly be regarded as an edaphically determined variant within the UPPER MONTANE rain forest formation.

It is interesting that the families of trees and shrubs involved in the different forest types show considerable parallels with those in other parts of the world. For example, those present in the MOR RIDGE forest are much the same as those in the UPPER MONTANE rain forest on peat in Malesia (Aquifoliaceae, Araliaceae, Clethraceae, Ericaceae, Guttiferae, Lauraceae, Melastomataceae, Myrsinaceae, and Podocarpaceae). The most notable absentees in the Jamaican MOR RIDGE forest are the Myrtaceae and Theaceae (both frequent in the MULL RIDGE forest) and the Symplocaceae (generally rare in Jamaica, cf. Adams, 1972). The most surprising family found to be represented is the Euphorbiaceae, with two abundant species, *Alchornea latifolia* and *Chaetocarpus globosus*. Of the three other families of trees present in the MOR RIDGE forest, the Cyrillaceae are found only in the New World, while the Myricaceae and Rhamnaceae were represented at our sites by only one individual each.

The 15 families represented by trees and shrubs, absent from the MOR RIDGE forest but present in MULL RIDGE — WET SLOPE forest, are also widespread in montane forests of the tropics. Those marked by asterisks in the following list are found in the UPPER MONTANE rain forest, with mull humus at relatively high altitudes, in the Andes [10] and/or New Guinea (cf. Cuatrecasas, 1958; Grubb & Stevens (in press)): Celastraceae,* Chloranthaceae,* Compositae,* Flacourtiaceae,* Gentianaceae,* Gesneriaceae,* Meliaceae, Myrtaceae,* Oleaceae,* Piperaceae,* Rubiaceae,* Sapotaceae, Solanaceae,* Staphyleaceae, and Theaceae.* The three families not marked by asterisks are typical of LOWER MONTANE as opposed to UPPER MONTANE rain forest on the higher equatorial mountains. All of the families mentioned in the previous paragraph (apart from the

[10] The *selva andina* of Cuatrecasas is almost certainly equivalent to our UPPER MONTANE rain forest and his *selva subandina* equivalent to our LOWER MONTANE rain forest.

Cyrillaceae) are also found in the higher-altitude UPPER MONTANE forests of the equatorial mountains.

The DRY SLOPE forest is particularly interesting because of the dominance of genera with marked dry-climate connotations. The following seven species belong to genera notable for their success in the Mediterranean-climate regions of Europe or California or in the neighboring mountains: *Garrya fadyenii*, *Juniperus barbadensis*, *Myrica cerifera*, *Rhamnus sphaerospermus*, *Satureja viminea*, *Viburnum alpinum*, and *V. villosum*. *Daphnopsis* is closely related to *Daphne*, which is also, in part, a Mediterranean-Montane genus. *Baccharis scoparia*, the switch plant, has many relatives in the dry inner valleys of the high Andes. In the case of *Dodonaea viscosa*, the same species is found on some of the drier slopes of the high mountains of equatorial South America and Africa.[11] Of the remaining species, *Bidens shrevei*, *Eupatorium parviflorum*, *E. triste*, and *Vernonia divaricata* are soft-leaved shrubs representative of a family (the Compositae) which is widespread on the limestone at lower altitudes in the dry southwestern part of Jamaica.

At present the mean annual rainfall in the DRY SLOPE forest is quite high (up to 2700 mm.), well over the 1400 mm. needed to sustain rain forest ("MOIST MONTANE" forest) in the Lower Montane Zone in Africa (Zamierowski, 1975) and even well above the 1800 mm. generally needed to sustain rain forest in the tropical lowlands (Richards, 1952). Before man opened up the community, there was probably a continuous forest made up of characteristic DRY SLOPE trees (*Brunellia*, *Daphnopsis*, *Myrica*, *Myrsine*, *Oreopanax*, *Rhamnus*, and *Viburnum*) and some of the MULL RIDGE and WET SLOPE trees (mainly *Alchornea*, *Clethra*, *Cyrilla*, *Ilex*, and *Vaccinium*). At that time the *Dodonaea viscosa*, the *Juniperus barbadensis* Thunb., and the various shrubs now so prominent (species of *Baccharis*, *Bidens*, *Bocconia*, *Eupatorium*, *Satureja*, and *Vernonia*) may have been more or less confined to rock outcrops or to land slips. The DRY LIMESTONE scrub forest on the southeast slope of John Crow Peak at the present time illustrates one natural habitat for several of the species. If the climate during the last Ice Age was much drier than it is at present in Jamaica, as seems to have been the case in South America (Vuilleumier, 1971), Africa (Van Zinderen Bakker & Coetzee, 1972; Hamilton, 1974), and northeastern Australia (Kershaw, 1970; 1974), the DRY SLOPE forest is likely to have been more widespread and the light-demanding shrubs may have grown widely on ordinary slopes as well as on rock outcrops.

It is also important to consider past climates in interpreting the distinctly subalpine features of leaf form and life form found in the HIGH ALTITUDE forest (cf. p. 340). If the forest limits were lowered by 1000 meters in the last Ice Age (cf. Walker, 1970; Vuilleumier, 1971; Flenley, 1972; Van Zinderen Bakker & Coetzee, 1972), the top of Blue Mountain Peak (now 2265 meters) would have reached a level at which SUBALPINE forest is found today in parts of the Andes (Vareschi, 1955). The colony

[11] In New Guinea it is found on river gravels, on natural forest margins, and in secondary forest (Grubb & Stevens, in press).

of the tussock grass *Danthonia domingensis* ("*D. shrevei*") at about 1850 meters on the north side of High Peak (named Sir John Peak in Shreve's account) could be a relict of this period, but the factors controlling its persistence at the present time (and its absence from the appreciably higher Blue Mountain Peak) are obscure. Shreve (1914) reported that there is nothing obviously peculiar about the soil where the plant grows, but he noted the low growth of the trees and shrubs mixed with it.

Unfortunately we have made no new observations on the downward continuation of the MONTANE rain forests in Jamaica, and we can relate the lower-altitude types to the schema in TABLE 1 only on the basis of Asprey and Robbins's (1953) account and certain new facts provided by C. D. Adams (pers. comm.).

The major component of the "MONTANE MIST" forest of Asprey and Robbins is our MULL RIDGE — WET SLOPE forest, but it also includes our MOR RIDGE forest and GULLY forest. The lower limit of the "MONTANE MIST" forest on the northern slopes of the Blue Mountains is said to be at about 3500 feet (1050 meters), and this is presumably the lower limit of our UPPER MONTANE rain forest in that area. In the John Crow Mountains, which are wetter, there is a gradual transition from LOWER MONTANE rain forest at 700 meters to LOWER MONTANE — UPPER MONTANE transitional forest at 900 meters and possible UPPER MONTANE (Limestone Pavement) forest above 950 meters.

There seems to be a continuum in structure, physiognomy, and floristics between our GULLY forest at about 1500 meters on nonlimestone rocks in the Blue Mountains, our WET LIMESTONE forest at 700 to 800 meters in the John Crow Mountains, and the "LOWER MONTANE" rain forest described by Asprey and Robbins from sites at 550 to 750 meters on the slopes of the Rio Grande Valley between the Blue Mountains and the John Crow Mountains. It would appear that the forest is commonly 24 to 30 meters in height at an altitude of 550 to 750 meters. Asprey and Robbins report three species (*Ficus maxima* ('*suffocans*'), *Psidium montanum*, and *Symphonia globulifera*) as emergents to 36 meters near the lower limit, but according to Adams none of these species can be considered characteristic of this forest type and none grow commonly to more than 30 meters tall.

There is a further continuum in structure, physiognomy, and floristics from the "LOWER MONTANE" rain forest of Asprey and Robbins at 550 to 750 meters in the Rio Grande area to their "WET LIMESTONE" forest at 300 to 750 meters in the Cockpit Country, an area of karst limestone in the western part of the island, and in a similar area near the center of the island rising to 838 meters in Mt. Diablo (see FIGURE 1). Their "WET LIMESTONE" forest is described as about 18 meters tall with relatively few emergents to 30 meters; the trees do not have large buttresses. Asprey and Robbins's account suggests that thick-stemmed lianas are absent, but *Rourea glabra* (*R.* "*paucifoliolata*"), reported by them, can grow to a height of 30 meters and develop quite thick stems (Adams, 1972). Moreover, according to Adams (pers. comm.), there are other

species present with substantial stems, e.g., *Chamissoa altissima*, *Clematis dioica*, *Ipomoca ternata*, and *Schlegelia parasitica*. Usually these species attain a DBH of no more than about 5(–10) cm. Taking the criteria of TABLE 1 as a whole, this forest must be assigned to the LOWER MONTANE rain forest formation.

It is notable that the forest contains a number of woody families usually more or less confined to lowland forests in other parts of the tropics: Anacardiaceae (*Comocladia* and *Mosquitoxylum*), Annonaceae (*Annona*, *Oxandra*, and *Xylopia*), Burseraceae (*Bursera*, rare in wet areas), Canellaceae (*Cinnamodendron*), Combretaceae (*Buchenavia*, *Bucida*, and *Terminalia*), Nyctaginaceae (*Neea* and *Pisonia*), Quiinaceae (*Quiina*), and Simaroubaceae (*Picrasma* and *Simarouba*). Of the genera listed here only one (*Oxandra*) was recorded by Asprey and Robbins from their "LOWER MONTANE" rain forest and only two (*Neea* and *Picrasma*) were recorded by us. However, all of the others except *Mosquitoxylum*, *Bucida*, and *Simarouba* are noted by Adams (1972) as being found, at least occasionally, above 2000 feet (about 600 meters). It thus appears that the lower part of the LOWER MONTANE rain forest in Jamaica shows the *mélange* effect of Grubb (1974) and Grubb and Stevens (in press) to a marked degree, i.e., the particular forest type, defined on structure and physiognomy and found at a lower altitude than it would be on a high mountain in the equatorial belt, contains floristic elements that are confined to lower-altitude forests in the high equatorial mountain situation. The same effect is seen in the LOWER MONTANE rain forest at 150 to 600 meters in Puerto Rico discussed in the work edited by Odum and Pigeon (1970) and in the LOWER MONTANE rain forests at 260 to 800 meters on various Caribbean Islands discussed by Beard (1944, 1955).

There is no typical LOWLAND rain forest, as defined by TABLE 1, in Jamaica at the present time. Possibly it existed at or near sea level before the coming of man in the areas with an annual rainfall of more than 1800 mm., e.g., where sugarcane is now grown. However, Adams believes that it would probably have been a marsh forest variant of LOWLAND rain forest. He says that the last remnants of high forest of this type at and near sea level are being destroyed at present in parts of the parishes of Westmoreland and Hanover in western Jamaica. Components include *Bucida buceras*, *Crudia spicata*, *Symphonia globulifera*, *Tabebuia angustata*, and *Terminalia latifolia*, with the massive liana *Dalbergia brownei*. A similar forest in the Black River plain in the parish of St. Elizabeth has, in addition, *Grias* (cauliflorous) and large bignoniaceous vines. These forests are the nearest in Jamaica to the LOWLAND rain forest associated with the great rivers of South America (cf. Adams, 1971, p. 56), but they are subject to distinct seasonal and edaphic constraints.

In summary, LOWLAND rain forest in the sense of TABLE 1 may have existed in the past in a few areas at an altitude below 300 meters, but it is now virtually impossible to be sure. The few remnants of high forest at or near sea level are of a distinctly marshy type. Relict areas of LOWER MONTANE rain forest are still found from 300 meters to 1750

meters. In the lower part of its range this forest type occurs on ridges and slopes, as well as in gullies, and it contains a wide range of species. Many of the woody families present have strong lowland affinities. At the upper end of its range this forest type is confined to gullies and is much poorer in species. On the slopes of the John Crow Mountains there is a continuum from LOWER MONTANE rain forest at 700 to 800 meters to what must probably be classified as UPPER MONTANE rain forest above 950 meters. The transition from LOWER MONTANE to UPPER MONTANE rain forest on the slopes of the Blue Mountains has not been studied in detail but apparently occurs at about 1050 meters. The UPPER MONTANE formation contains at least four different associations: MOR RIDGE forest (local in occurrence), MULL RIDGE — WET SLOPE forest (very widespread with a local VERY WET RIDGE forest *facies*), DRY SLOPE forest (formerly widespread, now mostly destroyed), and HIGH ALTITUDE forest (found only above 1850 meters and confined to a few peaks). These four forests are closely similar in structure and physiognomy to UPPER MONTANE rain forests elsewhere except for their possession of approximately equal numbers of tree and shrub species with microphylls and notophylls. They are also similar in their content of woody families, but they do contain a few families more characteristic of LOWER MONTANE forests in equatorial regions.

DEVELOPMENT OF THE MOR RIDGE FOREST

It is necessary to justify the term "mor," because many observers would describe the relevant soils in the Blue Mountains as "peat." In that part of Europe neither strongly oceanic nor strongly continental, e.g. southeastern England, mor and peat are quite distinct. Peat is formed under topographically determined waterlogged conditions; the drainage waters may be base-rich and the pH of the peat high or the waters may be base-poor and the pH of the peat low. In either case microbial breakdown is primarily inhibited by the waterlogged conditions. In contrast, mor is formed on strongly leached upland sites, nearly always on base-poor parent materials; the pH of the uppermost mineral soil where mor begins to form is always strongly acidic (pH less than 4.5, usually less than 4.0). The soil is more or less freely drained, and microbial breakdown is primarily inhibited, either by factors related to the low pH as such or by various phenolic compounds present in large quantity. Accumulations of mor humus seen in southern and central England at the present time are usually only 5 to 10 cm. thick (Watt, 1934; Ovington, 1954; Dimbleby & Gill, 1955; Mackney, 1961; Gimingham, 1972). However, accumulations 20 to 30 cm. thick under *Quercus* species and *Castanea sativa* Mill. have been found by O. Rackham (unpublished data) and similar accumulations (some more than 70 cm. thick) are known in Germany, Denmark, and Norway (Iversen, 1964). It appears that most sites at which such accumulations developed have been destroyed by human activity.

In the strongly oceanic parts of Europe, especially in the mountains (e.g., in western Ireland, Wales, and Scotland), the distinction between mor and peat becomes less clear. Acidic "blanket peat" develops over most surfaces where precipitation normally exceeds evaporation. Even in such areas normal podzols with mor humus are commonly found on the upper parts of steep slopes grading into thin iron-pan soils covered by peat on the ridges and deep peat-gley soils on the plateaux and dip slopes (Crompton, 1952; Crampton, 1963; Holding, Franklin, & Watling, 1965).

Even where forest mor and forest peat are quite distinct topographically, they are often similar in micromorphology. Both materials commonly contain substantial quantities of undecomposed plant fragments (parts of leaves, twigs, fruits, and pollen) and fungal hyphae. However, mor typically contains an appreciable fraction made up of the fecal pellets of mites (Kubiena, 1953; Kendrick & Burges, 1962), the actual proportion being higher in some kinds of mor than in others (Iversen, 1964). Peat frequently contains obvious remains of mosses, but only in certain bog-peats is the bulk of the material derived from them. Both mor and peat may become matted and both often blacken with age.

On well-drained soils in the lowland tropics there are many known occurrences of deep mor humus accumulations quite distinct from peats, e.g., in Borneo (Hardon, 1937; Richards, 1962, 1965; Brunig, 1969), in Guyana (Richards, 1952), and in Brazil (Klinge, 1965). There are also obviously waterlogged acid peat deposits, e.g., in Borneo and Sumatra (Polak, 1933; Coulter, 1950, 1957; Richards, 1952; Anderson, 1963, 1964). Intergrades between mor and peat do not seem to have been recorded explicitly but very probably occur in Borneo (cf. Brunig, 1969).

Despite the existence of topographic intergrades and resemblances between mor and peat in micromorphology, most organic accumlations can be ascribed to one or the other type on the basis of the genesis of the material, whether it is controlled primarily by waterlogging (peat) or by extreme acidity without waterlogging (mor).

In the UPPER MONTANE forest in Jamaica, surface accumulations of organic matter are not found in any of the manifestly very wet sites — on limestone in the John Crow Mountains, in GULLY forest or the HIGH ALTITUDE forest of the Blue Mountains, or in the VERY WET RIDGE forest of Mt. Horeb. This suggests that the accumulations that are found are not determined primarily by waterlogging.

However, the possibility of waterlogging in the upper layers of the soils on the knolls bearing MOR RIDGE forest has been considered carefully. During a year's observations it was found that the knolls certainly were not regularly in fog when the other parts of the ridge were free of low cloud (obs. E. V. J. T.). Indeed there is indirect evidence that the atmosphere within the forest on knolls was actually drier, largely as a result of the more open canopy — the *minimum* temperatures were lower and the maximum higher (obs. E. V. J. T.). Shreve's (1914) records emphasized the frequent occurrence of low relative humidities on the ridge forests, and this has been specifically confirmed by one of us (E. V. J. T.)

for a MULL RIDGE site. The accumulated organic matter was, of course, saturated after rain had fallen, but it was frequently less than saturated during sunny spells. There is no sign of gleying in the mineral soil beneath it. The only possible indicator of wetter conditions in the MOR RIDGE forest is the greater development of epiphytes, but we attribute this to the sloping trunks offering more suitable sites for establishment, the open canopy providing a more favorable light-climate at the level of the trunks, and, possibly, a greater average age for the trees affording a longer time for colonization.

While the evidence is against the involvement of waterlogging, there is a strong correlation between the degree of accumulation of organic matter and the pH in ridge soils — only 1 to 2 cm. in depth in the top of the "mineral" soil on Mt. Horeb (pH 4.2), through the top 5 to 10 cm. of the "mineral" soil in the MULL RIDGE forest of the Morce's Gap area (pH 3.5–4.0), and up to 50 cm. above the "mineral" soil in the MOR RIDGE forest of the same area (pH 2.8–3.5).

There is a basic difficulty in interpreting this correlation as evidence that humus accumulation is dependent on low pH, since the pH is unquestionably dependent on the accumulation of humus — the more humic acid carboxyl groups present and not occupied by bases, the lower the pH. This precise situation is met in the North Temperate Zone (see, for example, Gorham, 1953, for the Lake District in N. W. England). The usual analysis of the situation is based on the idea of a self-generating or autocatalytic system. It is generally supposed that once leaching of the topsoil has reached a certain critical level, there are important changes in the availability of major mineral nutrients (N, P) and that shortage of these induces the formation of mor-forming litter. The mor-forming litter (or even the living canopy) is then supposed to release substances which inhibit the microbial release of mineral nutrients still further, and so a stagnated system develops (cf. Handley, 1954; Coulson *et al.*, 1960; Davies *et al.*, 1964). An alternative explanation involves the mycorrhizal fungi of the dominant trees in the inhibition of the mineral-releasing and litter-decomposing microbes (Gadgil & Gadgil, 1971). Both hypotheses are useful in providing models of a self-generating system, and either could be applied to the Blue Mountain system. Many early stages in the development of mor were found, and there can be little doubt that there is an inevitable trend from mull to mor on the ridge near Morce's Gap at the present time.

One particularly interesting feature of the situation in the Blue Mountain forests is the considerable number of tree species which can produce mull or mor humus, depending on the soil conditions. This is reminiscent of the position in certain species-rich temperate deciduous forests of eastern North America (cf. Chandler, 1941).

In the North and South Temperate Zones certain trees and shrubs have the ability to acidify soils particularly rapidly and so precipitate the onset of mor formation (Watt, 1934; Scott, Thomson, & Simpson, 1936; Ovington, 1953; Burges & Drover, 1953; Grubb & Suter, 1971). There is

no evidence that any of the species in the Jamaican montane forest have this ability; the processes of mor formation appear to be set in motion simply as a result of generalized leaching of the type, which occurs inevitably under any plant canopy where precipitation exceeds evaporation.

The only other case recorded from a tropical mountain in which mor is formed without any intergrading to peat is that reported by Pitt-Schenkel for LOWER MONTANE rain forest (*sensu* our TABLE 1) at about 1650–2280 meters in the western Usambara Mountains in Tanzania, where the annual rainfall is about 1250 to 1600 mm. (i.e. distinctly less than in the Blue Mountains) and rather markedly seasonal. The bedrock is gneiss. The mor humus (A_1 horizon of Pitt-Schenkel, 1938, p. 76) is about 10 to 12 cm. thick and has a pH of 3.0–3.2. The A_e horizon below it (A_1/A_2 of Pitt-Schenkel) is a friable loam with bleached quartz grains (pH 3.2–3.4). This African soil type is in need of more comprehensive investigation, but it appears to differ from that in Jamaica by the thinness of the mor layer and the presence of a clearly leached mineral layer. It is notable that although the forest trees do not grow as tall as those on mull sites elsewhere, most of the tallest individuals are still 23 to 24 meters tall.

The mor of the Usambara Mountains in Tanzania and the Blue Mountains in Jamaica may be contrasted with the peat found on mountains in Borneo, the Solomon Islands, Malaya, and New Guinea.

Askew (1964) described the development of peat on ridge crests of a shale/sandstone formation under heavily mossed forest (almost certainly UPPER MONTANE rain forest *sensu* TABLE 1) at about 1800 to 2700 meters on Mt. Kinabalu in North Borneo. The soil surface and tree branches were said to be "completely mantled in a thick layer of moss." The peat is very dark reddish brown, about 40 cm. thick, and has a fine-sized granular structure. The "pH" is recorded as 2.3; this is a pH measurement made in KCl solution (G. P. Askew, pers. comm.). A pH_{H_2O} value of 3.4 is given by Burnham (1974). Beneath the peat is a markedly gleyed, eluviated horizon, but only at certain sites are iron pans present.

Of particular interest in the present context is the transition from peat and gleying at 1800 meters to fibrous mor and nongleyed podzols under much less mossy forests at 1500 meters. Askew (1964, p. 69) describes the transition as gradual — it corresponds with the transition from UPPER MONTANE rain forest to LOWER MONTANE rain forest ("SCLEROPHYLLOUS MOUNTAIN" forest). Askew also records a fascinating series of stages of increasing mor development with the increase in altitude. At about 1250 meters thin mor and micropodzols are found only on the gentler sloping sites of ridge crests, but with the increase in altitude the mor layers and eluviated horizons thicken and spread to steeper sites. The pH_{KCl} of the mor is 2.0 and that of the eluviated mineral horizon 2.8; the organic carbon content of the mor is 40 per cent, about the same as in the peat. Askew, following Mohr and Van Baren, attributes the greater development of mor to a direct effect of temperature on litter decomposition. We would challenge this view. Mor formation can occur without doubt at

sea level (cf. Hardon, 1937; Klinge, 1965; and others), and it seems more likely to us that the effect of temperature is mediated through the plants; under the increasingly less favorable growing conditions (lower temperatures and more cloud), either they produce litter more and more completely determined as potential mor (e.g., through a higher content of polyphenols), or their mycorrhizas are increasingly strong competitors with the micro-organisms which might otherwise decompose the litter.

One curious feature of the zone of peat-forming forest is the occurrence of mull soils rather than mor soils on the slopes. The situation is markedly different in this respect from that described for parts of oceanic Britain (Crompton, 1952) and from that in the Solomon Islands.

Lee (1969) has described in some detail the soils of Kolombangara in the western Solomon Islands. On the summit slopes of Kolombangara (1550 meters) there occurs what is probably one of the most continuously fogged UPPER MONTANE rain forests in the world. The rainfall is estimated at about 3000 mm. and is rather evenly distributed through the year, but the consistent fog is probably of more importance in pedogenesis. The bryophytes completely cover the trunks and major branches to a height of at least 3 meters and exaggerate the apparent DBH by more than 20 per cent (P. J. G. & T. C. Whitmore, unpubl. obs., 1963; see also Whitmore, 1969). The bedrock is andesite. On the ridges above 1000 meters a very dusky red, very greasy, and very wet moss peat is found; the pH is 3.0–3.3 and the thickness generally 10 to 20 cm., reaching 40 cm. at the summit. At most sites there is under this peat an eluviated and gleyed horizon; near the summit a very thin iron pan is found beneath the eluviated layer. It is particularly interesting in the present context that the uppermost slope sites beneath the UPPER MONTANE rain forest on the ridges were described by Lee as having accumulations of mor rather than peat (5 to 9 cm. thick). The pH of the mor is given for one site as 3.25 and the loss-on-ignition is 82 to 95 per cent. The texture varies considerably, as one might expect of a mor/peat intergrade, at one site "fibrous," at another "greasy," and at a third "peaty." There does not appear to be any obvious eluviated layer below it, where the mineral soil has a pH of 3.5–5.0. Apart from this lack of obvious podzolization under the mor, the situation is clearly very much like that described from oceanic parts of Britain by Crompton (1952).

In Malaya most UPPER MONTANE rain forest is found growing on peat, although there are some sites where it is not found (Holttum, 1924; Whitmore, 1975). Whitmore and Burnham (1969) have given an elegant account of the transition on granite from yellow latosol supporting LOWLAND rain forest at 300 meters to a peat soil supporting UPPER MONTANE rain forest at 1500 to 1600 meters. The annual rainfall in the area which they describe is about 2500 mm. Although this is distinctly seasonal, it is believed that frequent fogging in the season with less rainfall ensures that the soil very rarely dries out. Bryophytes are frequent on the forest floor in the better lit sites, but they extend up the trunks generally only

to about 1 meter and do not form as thick a cover as on Kolombangara. The peat covers all the ridge and plateau sites, often 20 to 50 cm. thick and sometimes 1 meter thick. It is black, massive, spongy, greasy, and lacking in pores. Beneath it there is a very wet eluviated layer (A_e) and beneath that an iron pan; very often the A_e layer is distinctly gleyed. The peaty podzol soils are thus very much like those described from Mt. Kinabalu and Kolombangara.

In the upper part of the Malayan LOWER MONTANE rain forest (above about 1200 meters), there is frequently a rather thinner surface accumulation of organic matter, termed "peaty" by Whitmore and Burnham but distinguished by them as dusky red rather than black, as friable and not greasy, and as having a considerable inorganic component. During a visit with Dr. T. C. Whitmore in 1970, one of us (P. J. G.) suggested that the deposit might better be described as a hydromor. We found at several sites in the Cameron Highlands a marked eluviated layer beneath but no obvious illuviated layer or gleying, much as in some of the iron podzols described by Kubiena (1953). The pH of the putative mor was found to be 3.6 by Whitmore and Burnham and that of the mineral soil below it 4.6. The putative mor is found on the slope soils at the same altitude as the peat on the ridges, so the position in this respect is more like that on Kolombangara than on Mt. Kinabalu. However, there is apparently a tendency toward deeper mor formation with increasing altitude on the ridges below the zone of peat-formation, much as on Mt. Kinabalu.

The first report of typical podzol-profiles in the mountains of Southeast Asia was that of Hardon (1936) from the Vogelkop Peninsula of northwestern New Guinea. At an altitude of 2000 to 2400 meters in the Mt. Koebré area at the south end of the Arfak mountains, under what we would call UPPER MONTANE rain forest (cf. Grubb & Stevens, in press), typical podzols develop over shales and sandstone. The annual rainfall is believed to be between 1500 and 2500 mm., and persistent fog is very frequent. On the summit the "raw humus" cover consists of 40 cm. of gray-brown spongy fibrous peat over 30 cm. of brown compacted peat. On the lower slopes, which have been much affected by man, the "raw humus" cover is only 20 to 25 cm. thick. It is not clear whether any areas carry well-defined mor as opposed to peat. Further east, in the main ranges of West Irian where the climate is similar, most "podsols" are said to have "moder" humus, while peat develops only in topographically suitable sites (Haantjens, Reynders, Mouthaan & Van Baren, 1967, pp. 36, 37). Even further east, in Papua-New Guinea, true peats appear to be rare in the Montane Zone (cf. Grubb, 1974).

The gradation between peat and mor is thus poorly documented for New Guinea, but a spectrum of humus types has been shown clearly to exist in the other three areas of Southeast Asia considered. The existence of this spectrum of types of humus accumulation must be taken into account when schemes are put forward to explain the mechanisms of accumulation.

SPECIES GROUPS AND LIMITING FACTORS

As a result of our floristic account, summarized in TABLES 2 and 3, we can isolate various groups of species and consider the factors most likely to be limiting their distribution.

First we have the species recorded only from low altitude LOWER MONTANE rain forest. The information available is least complete for these species, but since there appears to be a continuum of change in floristic composition with altitude in a single kind of topographic site (e.g., gullies in the Blue Mountains), it is suggested that some function of temperature is the effective factor limiting the upward spread of these species.

It is convenient to consider next three groups of species: (a) those exclusive to LOWER MONTANE (GULLY) forest at higher altitudes (e.g., *Bochmeria caudata*), (b) those much more frequent and much taller in such forest (*Solanum punctulatum* and other GULLY species in TABLE 2), and (c) those about as frequent in LOWER MONTANE (GULLY) forest at 1500 meters as on slopes and ridges but less tall in the latter situations and most markedly reduced in performance in MOR RIDGE forest (the "core" species of TABLE 2). For these three groups, presence and performance at their upper limit are strongly related to topography, and it seems most unlikely that temperature determines the upper limit. Neither air temperature nor leaf temperature seems to be responsible, since there is no evidence of the ridges or slopes being more subject to fog than the gullies. Wind is not involved, because wind-pruning, which is distinct when it occurs, was seen only at certain sites on the steep north-facing slopes from Portland Gap toward Blue Mountain Peak and on knife-edge ridges in HIGH ALTITUDE forest.

Shreve emphasized the favorable water supply in the gullies, and we accept that there is a more favorable supply than on ridges and slopes; however, we do not consider water supply to be a limiting factor for trees and shrubs on the slopes or ridges after the seedling stage. Furthermore, the characteristic GULLY species do not appear in the VERY WET RIDGE forest on Mt. Horeb, where instead we see different wetness indicators, such as *Cephaelis elata* and *Selaginella denudata*.

The penetration of lower altitude species to their highest limits in gullies is very commonly observed on tropical mountains. It is also seen in the North Temperate Zone, where it can be related, at least in some cases, to the incidence of flushed soils in the gullies and leached soils on the ridges (Gorham, 1953). More generally, many species in Europe are restricted to more fertile sites at the northernmost edge of their range (see, for example, McVean & Ratcliffe, 1962; Stalfelt, 1972), and many species can be established artificially if the soil is limed and N, P, and K are added (cf. Miles, 1974). Superficially, the situation in Jamaica appears to parallel this classical leaching situation — some species are confined to the flushed sites, others are much more frequent and taller on them, and yet others show a response in performance but not obviously in frequency.

One field observation strongly suggests a role for nutrient supply. On the slopes of John Crow Peak at about 1500 meters, below the limestone but above the last small gap in the ridge, the forest is much taller than the widely distributed WET SLOPE forest described above (p. 333) and buttresses 0.5 meters tall are common; the pH of the topsoil is 4.7 to 4.8. Unfortunately we have no information on the tree species present. The most obvious explanation for the occurrence of this forest is that it benefits in some way from the leaching of the limestone above it.

The foliar analyses for "core" species at different sites (TABLE 5) yield some evidence to support the hypothesis that nutrient supply is more favorable in gullies than on slopes and ridges with mull humus. K levels are higher in gully material of both *Alchornea* and *Clethra*, but there are no consistent differences in N or P. Tropical forest soils seem generally to differ from temperate forest soils in showing not only plentiful mineralization of nitrogen but also abundant production of nitrate at very acid sites (pH 4.0–4.5, see Cunningham, 1962; De Rham, 1971), and we should perhaps not expect a significant difference between GULLY and SLOPE soils in this respect. However, the MULL RIDGE soils are significantly more acid yet (pH 3.5–4.0), and apparently nothing is known of the mineralization characteristics of such soils. The lack of apparent difference in P status may result from a very poor supply at all sites (owing to the various soil parent materials all being deficient in that element), or it may result from the mycorrhizas of the mature trees being so effective in uptake that any soil differences are hidden. Clearly much more research is needed on this problem. This should involve more extensive foliar analyses, tests on the mineralization of nitrogen in the soil, bioassays of the various soils with seedlings, and fertilizer experiments with adult plants *in situ*. Some work along these lines has been carried out by one of us (E. V. J. T.) and, after analysis, will be reported elsewhere.

The idea that mineral supply might limit the distribution of forest types on wet tropical mountains was put forward before (Grubb, 1971) as a possible explanation of the "Massenerhebung" effect, the occurrence of given forest types at lower altitudes on smaller, outlying mountains. At that time the implication was that the species of LOWLAND, LOWER MONTANE, and UPPER MONTANE forests are successively better adapted to poor mineral supply. Alternative partial explanations of the "Massenerhebung" effect have since been put forward (Grubb, 1974; Grubb & Stevens, in press). The present suggestion does not imply that LOWLAND, LOWER MONTANE, and UPPER MONTANE species necessarily have different mineral requirements according to some absolute standard, but that at the upper limits of their distributions there may be an interaction between mineral supply and climatic factors such that mineral supply (determined by topography) can become the chief limiting factor.

The next species group to be considered is that confined to MULL RIDGE and WET SLOPE forests (TABLE 2). By analogy with what is established for vegetation in other parts of the world, we suggest that

some aspect of competition keeps several of these species out of the gullies, where they would probably grow very well if all other plants were removed. Their upper limit is not obviously related to topography, and some function of temperature is likely to be limiting — possibly leaf temperature rather than air temperature, since fog is definitely more frequent in the HIGH ALTITUDE forest from which they are absent. The same temperature limitation applies to three of the six "core" species and many of the DRY SLOPE species (TABLE 2).

Of particular interest is the failure of the MULL RIDGE and WET SLOPE species (TABLE 2) on the mor humus soils and the distinctly poorer performance of the "core" and MOR RIDGE species there. Some idea of the complexity of the chemical factors likely to be limiting growth on the mor humus can be gained by reviewing the work done on growth of crops on very acid lowland peat in Indonesia and Malaya. As a general rule it is necessary not only to add large amounts of lime to raise the pH to a value greater than 4.5, but also to add nitrogen, phosphorus, potassium, and copper (Polak, 1948). A few crops will grow in unlimed peat, e.g., pineapple, which responds to N, K, and Cu (Allen & Coulter, 1957; Parbery & Venkatachalam, 1964), and tapioca, which responds to N, P, and S, but not to K (Lim, Chin, & Bolle-Jones, 1973). There is also variety in the responses of crops that grow only after liming. Wet padi has an overwhelming requirement for P (Allen & Coulter, 1957); sweet potatoes need additional N and K, but do not respond when P alone is added (Chew, 1970); and tomatoes need not only N, P, and K, but also Bo (Joseph, Serrat, & Williams, 1970).

By analogy with the above results, we may suggest that the failure of MULL RIDGE and WET SLOPE species on mor results from the low pH as such. The fact that the pH is so low (< 3.5) suggests that the exchange sites are mostly saturated with hydrogen, since aluminum, when present, is an effective buffer to pH ca. 4.2 (cf. Jackson, 1963). Thus the undoubted toxicity of aluminum ions for many plants invading soils of pH < 4.8 (cf. Grime & Hodgson, 1969) is unlikely to be relevant here. Rather, the high concentrations of hydrogen ions are likely to be toxic as such; many plant cells are damaged in the laboratory at pH < 4 and are unable to absorb mineral nutrients (Arnon & Johnson, 1942). Clearly, experiments with seedlings of MULL RIDGE and WET SLOPE species are needed. Even if the pH were raised to the range of 3.5–4.0, that found in the MULL RIDGE soils, there might prove to be a variety of nutrient deficiencies, depending on the species tested.

We have, from foliar analysis, some evidence of the mineral nutrients possibly limiting growth of the "core" and MOR RIDGE species, which can by definition tolerate the extraordinarily high hydrogen ion concentrations of the mor humus. The foliar analyses of *Alchornea* and *Clethra* (TABLE 5) show very low levels of K, and the small amount of K circulating in the forest has been amply confirmed by one of us (E. V. J. T.) through other lines of investigation. Effective limitation of plant growth by shortage of potassium on acid peats in the Northern Hemisphere has

been reported by Heikurainen (1964), Tamm (1964), and Goodman and Perkins (1968a, b), but it seems that no case of parallel limitation on mor has been reported. The failure of uptake of K in *Alchornea* and *Clethra* may be a result of hydrogen ion toxicity. It is notable that foliar Na levels are actually higher and, unless the exchangeable Na in the soil is unusually high, this suggests that the reduced K uptake is not explicable simply in terms of a low "K potential," i.e. low ratio of the chemical activity of K to the chemical activity of other cations. Such an effect would apply to Na as well as to K. It is perhaps surprising that the foliar levels of Ca and Mg are not particularly low in the *Alchornea* and *Clethra* from mor humus, but it was similarly found that the foliar levels of these elements are no lower in the trees of UPPER MONTANE rain forest on very acid peat in Malaya than in trees of LOWLAND rain forest on a deep latosol (Grubb, 1974).

There is no evidence for a poorer supply of P for either species analyzed, but there is some indication of a lower level of N in *Alchornea*. In the Temperate Zones one usually finds a shortage of mineralized nitrogen, especially nitrate, in mor humus (see results from widely separated areas reported by Pearsall, 1952; Handley, 1954; Zöttl, 1960; Ellenberg, 1964; Lemée, 1967; Lamb, 1975), but there are records of appreciable nitrification, at least at certain times of year, in various types of mor at pH 2.6–4.0 (Romell & Heiberg, 1931), in peat at pH < 4 (Klötzli, 1969), and in certain unusually acid mulls of pH 3.7–4.0 (Davy & Taylor, 1974; Runge, 1974). Samples of mor and acid peat from the lowland tropics contain appreciable amounts of ammonium, but generally low to very low levels of nitrate (Ellenberg, 1954; Richards, 1965). However, relatively high levels of nitrate were recorded from lowland peat in Malaya by Parbery and Venkatachalam (1964). Unfortunately it appears that no experiments on mineralization of nitrogen in such soils in the laboratory have been reported. While the soils will possibly nitrify readily, all of the nitrate may be taken up immediately by the plants or be very rapidly leached.

In some highly organic soils Cu and Zn can be so effectively adsorbed or chelated by the soil that they become limiting factors for plant growth (Polak, 1948; Allen & Coulter, 1957; Wallace, 1961; Kanapathy, 1972; Stalfelt, 1972); the analyses of *Alchornea* and *Clethra*, however, yield no evidence for their implication in the present situation. Possibly Bo is in short supply (cf. Joseph *et al.*, 1970).

At present we have no evidence that any chemical factor other than potassium shortage is implicated in the poor growth of the plants on the mor. However, it is likely that the very high concentration of hydrogen ions has a generalized effect in reducing the performance of even the plants that can tolerate it sufficiently well enough to survive. Much more analytical and experimental work is needed, and there may well be appreciable differences between species of forest trees, as there are between crop plants.

The HIGH ALTITUDE species are few in number (cf. TABLE 2). The

more or less strict confinement of most of them to high altitude sites strongly suggests that downward penetration is controlled primarily by temperature, although a requirement for continuously favorable water relations may possibly be involved.

The DRY SLOPE species seem to be absent from the WET SLOPE and MULL RIDGE forests, mainly as a result of competition; the few individuals of several DRY SLOPE species that are present appear to be very well grown. They do not seem to need drier conditions to grow well. This interpretation is supported by the occurrence of several DRY SLOPE species in HIGH ALTITUDE forest (cf. p. 340), where there is certainly more rainfall and more fog, but fewer species and possibly less "competition pressure." The most extreme example of a "competition-intolerant" species is *Bocconia frutescens*, whose major natural habitats are probably landslips and river gravels. It was seen on one fairly fresh landslip at 1470 meters with *Clibadium terebinthinaceum*, *Hedyosmum nutans*, *Trema floridanum*, and the rare *Tovaria diffusa*, as well as with *Lobelia assurgens*, *L. caudata*, and *Pityrogramma tartarea*. *Hedyosmum nutans* also invades DRY SLOPE and MULL RIDGE forest occasionally. Care must be exercised in discussing "competition intolerance" in species like *Bocconia frutescens*. It may easily outgrow plants of other species of the same age, but it is a poor competitor over its whole life cycle, presumably dying young and invading established vegetation only with difficulty.

In summary, it is clear that the montane forests of Jamaica show great variety within a small area and provide fine opportunities for the investigation of critical factors limiting the distribution of particular species groups. More sophisticated observations will help us formulate the hypotheses more clearly, but the prime need now is for experimental studies.

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A RADIOCARBON DATED POLLEN DIAGRAM FROM THE ALLEGHENY PLATEAU OF NEW YORK STATE

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THE GENERAL PATTERN of late Quaternary vegetation change in the northeastern United States has been known for some time, but many chronological and interpretational details of the pollen record of this region still remain to be worked out. In New York State early studies (Cox, 1959; Deevey, 1943; McCulloch, 1939) established that late-glacial spruce-pine communities were replaced by postglacial forests rich in pine, which in turn gave way to forest communities with varying percentages of deciduous trees and hemlock. Few radiocarbon dates are available for these or earlier events, and their documentation by detailed pollen diagrams is inadequate for most parts of the state. For these reasons, a site in west-central New York, which we have named Belmont Bog, was selected for study.

Previous work in western New York (Miller, 1973) provides pollen diagrams with which to correlate results. Comparison with one diagram in particular, that from the Genesee Valley Peat Works, which is located 2 km. east of Belmont Bog, has allowed local and regional differences in the pollen record to be distinguished. The pollen diagram from the Peat Works has been difficult to interpret because the top of the deposit is truncated and because spruce zone assemblages contain abundant herb pollen. New data from Belmont Bog permit a reevaluation of these problems.

Sediments from Belmont Bog, which presumably is situated on Olean drift, the oldest recognized Wisconsinan till in the Northeast, contain seven pollen zones. Six levels in the deposit were radiocarbon dated, and where the sedimentation rate could be determined accurately, pollen influx values were calculated. Otherwise, absolute pollen frequencies are presented.

The record shows that tundralike vegetation existed around both sites for an estimated 3900 years (16,400–12,500 yrs. B.P.[1]) and was followed by a briefer period (12,500–11,000 yrs. B.P.) of open spruce woodland. About 11,000 yrs. B.P., pines began to dominate the vegetation, reaching maximum numbers 10,100 yrs. B.P. Hemlock replaced pine as the dominant forest tree about 8400 yrs. B.P. Surface samples indicate that the present virgin forests at Tionesta Scenic Area and Cook Forest in northwestern Pennsylvania are very similar to those that existed during later postglacial time in southwestern New York.

THE SETTING

Belmont Bog is located at 42°15′N and 77°55′W in Allegany County, New York. The bog covers an area of 2 ha. and is situated in the Phil-

[1] yrs. B.P. = radiocarbon years Before Present.

lips Creek Valley, 6.4 km. east of the Genesee River and 6.1 km. east of Belmont. The bog surface is at an elevation of 497 m.

Regional Glacial Geology

The oldest Wisconsinan deposit in western New York is the Olean drift (MacClintock & Apfel, 1944), the age of which is not known precisely. However, since Olean till overlies peat dated at 63,900 ± 1700 yrs. B.P. (Muller, 1964; Dreimanis & Goldthwait, 1973), the maximum age of the drift can not be greater than this.

On the western margin of the Salamanca re-entrant, an unglaciated area in southern Cattaraugus and Allegany counties, drift younger than the Olean has been distinguished (MacClintock & Apfel, 1944). The margin of this drift sheet has been traced continuously from the Kent terminal moraine in Ohio, and there is general agreement that Kent till is of late Wisconsinan (Woodfordian) age. Wood from a lacustrine deposit overlain by Kent till near Cleveland, Ohio, has been dated at 23,500 yrs. B.P., establishing a maximum age for the Kent advance (White, 1969).

The Lake Escarpment and Valley Heads moraines mark the next major Wisconsinan ice advance in New York State. Dreimanis and Goldthwait (1973) give the age of these moraines as early Cary. Connally and Sirkin (1973) accept an early Cary age and note that ice apparently remained at the Valley Heads position while retreating in the far western part of the state. Final withdrawal of ice from the Valley Heads position occurred prior to 14,900 ± 450 years ago (Calkin, 1970).

Glacial Geology of Allegany County

Allegany County is in the Genesee section of the glaciated Allegheny Plateau (Coates, 1974). Except for a small portion in the southwest corner (a part of the Salamanca re-entrant), the county was completely ice-covered during portions of the Wisconsinan. South of the town of Belvidere, Olean drift covers the valley of the Genesee River and surrounding uplands, including the site of Belmont Bog. The ice sheet which deposited this drift advanced from the northeast and receded northward unevenly (Muller, 1957). In the valleys active ice tongues retreated by backwasting, which often resulted in deposition of marginal kame terraces. Belmont Bog and the nearby Genesee Valley Peat Works are on such a kame terrace. The kame terrace near Belmont Bog is pitted with several kettles. The atypical shape of the basin and its depth profile (Figure 1) suggest the coalescence of two smaller basins.

As Olean ice retreated, a proglacial lake formed in the Genesee River Valley. This lake, Lake Wellsville, was about 24 km. long and had an outlet 1602 ft. above sea level which emptied into the Allegheny River watershed (Muller, 1957). Since the lower part of Phillips Creek Valley was undoubtedly flooded, the shore of Lake Wellsville must have

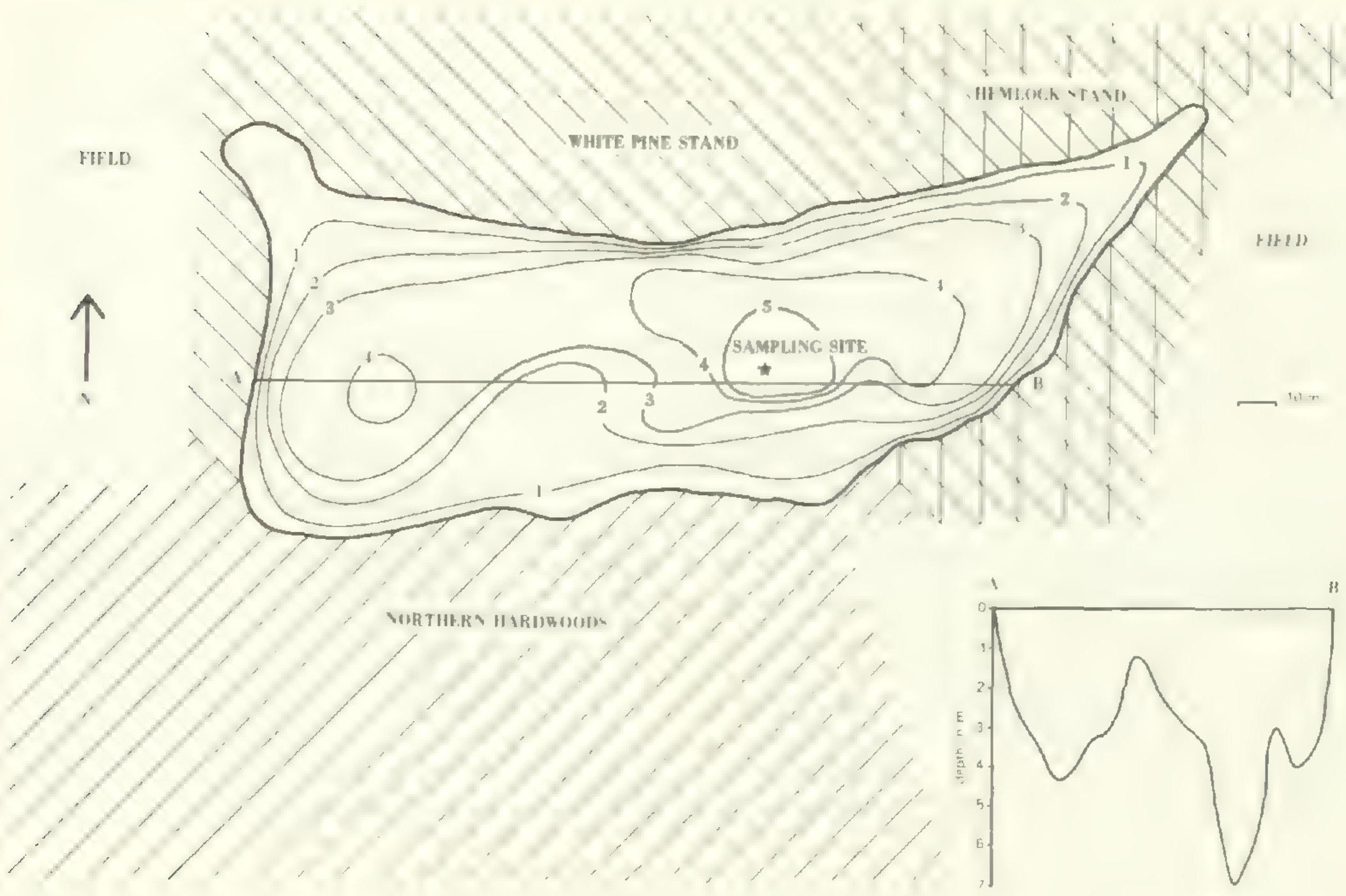

FIGURE 1. Basin of Belmont Bog showing depth contours (1 m. intervals), depths along east-west transect (A-B), and surrounding vegetation.

been close to Belmont Bog. After the ice retreated past Black Creek near Belfast, Lake Wellsville drained.

Kent drift covers the northern third of Allegany County. A lobe of the Kent ice advanced up the Genesee River Valley to within 4.8 km. of Belmont Bog and reestablished proglacial Lake Wellsville. Once the Black Creek outlet had reopened, Lake Wellsville drained and proglacial Lake Belfast-Filmore formed in the Genesee Valley. The Lavery drift and moraines recognized by Fullerton (1971) at East Rushford in the Genesee River Valley are thought by Muller (1957) to be deposits of a major stillstand in the recession of Kent ice.

During the Valley Heads advance, the ice sheet entered the northeastern corner of Allegany County to a point 10 km. south of Dansville. The margin of this ice sheet was about 35 km. northeast of the site of Belmont Bog. In the Genesee River Valley the Valley Heads terminal moraine is located at Portageville just north of Allegany County. A series of at least ten proglacial lakes formed in the Genesee Valley as the ice retreated northward to Mount Morris in Livingston County (Fairchild, 1908).

VEGETATION OF ALLEGANY COUNTY

Sketchy information exists about the forest vegetation of Allegany County prior to settlement by European man. Child (1875) and Minard (1896), who gathered reports from early settlers, indicate that white pine (*Pinus Strobus*) predominated in the forest and actually hindered clearing by its abundance. Hemlock (*Tsuga canadensis*), oak (*Quercus* spp.),

ash (*Fraxinus* spp.), elm (*Ulmus* spp.), chestnut (*Castanea dentata*), cucumber tree (*Magnolia acuminata*), and hickory (*Carya* spp.) were also common. Forests on bottomlands contained butternut (*Juglans cinerea*), buttonwood (*Platanus occidentalis*), cottonwood (*Populus* spp.), and elm.

A report from 1827 by a surveyor, Joseph Jones, recorded forest trees found in the Caneadea Indian reservation (Minard, 1896), which was located 23 km. north-northwest of Belmont Bog along the Genesee River. Bottomlands with alluvial soil had forests of elm, butternut, sycamore (*Platanus occidentalis*), and plum (*Prunus* spp.). Sandy loam soil of tablelands supported forests of white pine, white oak (*Quercus alba*), sugar maple (*Acer saccharum*), and birch (*Betula* spp.). Highlands with gravelly clay soil had pine and oak forest with chestnut and soft maple (*Acer rubrum*).

Original land surveys sometimes give a good description of forest composition and the names of witness trees. Unfortunately, original survey notes which might provide information useful in reconstructing presettlement forests apparently no longer exist for the eastern part of Allegany County where Belmont Bog is located. Gordon (1940), using original land survey data, topographic maps, soil surveys, historical accounts, interviews with old settlers, and field reconnaissance, has reconstructed the presettlement forest cover of adjacent Cattaraugus County. He recognized and mapped the following four major forest types which once covered most of that county. (Allegany County, which adjoins the eastern border of Cattaraugus County, no doubt had a similar forest cover.)

(1) Hemlock-white pine-northern hardwood forest covered the greatest area (see also Bray, 1915; Braun, 1950). The dominant trees were hemlock and beech (*Fagus grandifolia*); less frequent were sugar maple, yellow birch (*Betula lutea*), red maple (*Acer rubrum*), black birch (*Betula lenta*), and black cherry (*Prunus serotina*). Gordon (1940) recognized a separate Beech-maple component in Hemlock-white pine-northern hardwood forest, although he was unable to differentiate between the original distribution of the two and had to map them as one unit. Beech-maple forest occurred on the better drained soils of ridge tops, and dominant trees were sugar maple, beech, basswood (*Tilia americana*), white ash (*Fraxinus americana*), black cherry, and white pine. Beech-maple forest graded into (2) Mixed mesophytic forest, which occurred on well-aerated, moist soils. Dominant trees were red oak (*Quercus rubra* var. *borealis*), beech, chestnut, red maple, black birch, white ash, and black cherry. Cucumber tree, white oak, white pine, basswood, bitternut hickory (*Carya cordiformis*), sugar maple, hop hornbeam (*Ostrya virginiana*), and striped maple (*Acer pensylvanicum*) were less common species. Communities of Mixed mesophytic forest were transitional between Beech-maple and (3) Oak-chestnut forests, which occurred on high ridges and south and southwest slopes with dry soils. Dominant trees were white oak, red oak, chestnut, chestnut oak (*Quercus Prinus*), and

black oak (*Quercus velutina*). White pine, red maple, pignut hickory (*Carya glabra*), pin cherry (*Prunus pensylvanica*), black gum (*Nyssa sylvatica*), dogwood (*Cornus* spp.), and sassafras (*Sassafras albidum*) were less important. (4) White pine-American elm swamp forest occurred on river flats and flood plains. In addition to white pine and American elm (*Ulmus americana*), other common trees in the canopy were black ash (*Fraxinus nigra*), swamp oak (*Quercus bicolor*), red maple, hemlock, yellow birch, and white ash.

Goodlett and Lyford (1963) recognized two types of second-growth forest in the area immediately east of Allegany County. In the first, Northern hardwood, sugar maple, beech, basswood, hemlock, and white ash dominate. Red oak, red maple, yellow birch, and black cherry are less frequent, although they can be locally abundant. Gordon (1937) and Taylor (1928) have described the same type of secondary forest in Cattaraugus County. Gordon (1937) concluded that forests of this type occur in areas once occupied by presettlement hemlock-beech-northern hardwood and beech-maple forest communities. In present-day secondary Northern hardwood forest, hemlocks and white pines are greatly reduced in number because they were extensively cut for tanbark and lumber. The other kind of secondary forest recognized by Goodlett and Lyford (1963) is Oak forest. White oak characterizes this forest type, and red oak, white pine, black oak, chestnut oak, and large-toothed aspen (*Populus grandidentata*) are other dominants. Gordon (1937) recognized that this kind of oak forest replaced oak-chestnut, mixed mesophytic, and white pine presettlement forest communities in Cattaraugus County.

Flora and Vegetation of the Belmont Bog Area

A survey of forests in the Phillips Creek Valley was undertaken to establish the nature of forest vegetation near Belmont Bog. To determine importance values for dominant trees, two sets of thirty quarter points (Phillips, 1959) were done along transects on north- and south-facing slopes 1 km. south and 1.5 km. northwest of the bog respectively (Appendix A).

The north-facing slope is covered with forest of the Northern hardwood type. White oak is absent. Hemlock is in general less abundant than expected but is frequent on moist lower slopes with yellow birch. Sugar maple is abundant toward the top of the ridge. A deep ravine with what appears to be very old or possibly virgin forest was located at the end of the transect. The vegetation in this ravine appears similar to what Lewin (1974) has described as occurring in undisturbed ravines of the southern Finger Lakes region. A hemlock tree 100 ft. tall and 2 ft. in diameter at breast height was found near the top of this ravine.

Disturbed oak forest covers the south-facing slope. In this white oak is dominant; red oak is subdominant. The only hickory found was *Carya ovata*. No white pines occurred on the slope. The area had been lumbered within the last few decades, and most large trees had split trunks that

were unsuitable for timber. Tree tops and stumps littered the ground and the canopy was open.

A set of fifty quarter points was also done in forests immediately surrounding the bog to determine the dominant trees (see APPENDIX A). In sampled communities white pine was the most important tree, followed by hemlock, red maple, sugar maple, black cherry, beech, yellow birch, and red oak.

Although the quarter points have been tabulated in one unit, the forest can be divided into three parts (FIGURE 1). The first corresponds to stands of Northern hardwood forest. In it dominant trees are hemlock, sugar maple, red maple, beech, black cherry, red oak, and yellow birch. Seedlings and transgressives of nearly all these species can be found, and hence it seems to be a self-perpetuating unit. The other two units, one rich in hemlock and the other in white pine, are segregates of the Hemlock-white pine-northern hardwood forest type. Gordon (1937) reports that white pine or white pine mixed with hemlock occupied lower slopes, benches, and gravel terraces in the Allegheny River Valley. Similar stands of pure white pine or hemlock may have originally grown on the kame terrace on which Belmont Bog occurs. The hemlock unit occupies the eastern margin of the bog. Hemlock is dominant and few individuals of beech, yellow birch, and red maple were found. The transgressives are all hemlock trees. A thick layer of hemlock needles blankets the ground and no herbs have become established. The white pine unit consists of forest communities on the western and northern margins of the bog. The white pines appear even-aged and are mixed with a few black cherry, red maple, quaking aspen (*Populus tremuloides*), and red oak trees. There are a few young white pines in the subcanopy, but there are no seedlings of this species. Beech, hemlock, sugar and red maples are established under the white pine and probably will replace it in the next few hundred years, barring fire or windfall.

Compared with other bogs in western New York, the peat at Belmont Bog supports a very limited diversity of species. Trees, shrubs, and herbs around the margin are typical of bogs elsewhere in the region, but black spruce (*Picea mariana*) and tamarack (*Larix laricina*) are notably absent. Except for a marginal ditch, a sphagnum mat fills most of the basin. On it is established a leatherleaf (*Chamaedaphne calyculata*) heath. A few small white pine trees are growing on the mat. Red chokeberry (*Pyrus floribunda*), cotton grass (*Eriophorum virginicum*), pitcher plant (*Sarracenia purpurea*), and cranberry (*Vaccinium Oxycoccos*) are the only other common plants.

The flora of the Belmont Bog area is given in APPENDIX B.

LAND USAGE AND DEVELOPMENT

Child (1875) and Minard (1896) provide histories of the European settlement of Allegany County. Before the late eighteenth century, the Seneca Indians inhabited the area. They presumably had little effect on

the vegetation except along the alluvial flats of the Genesee River, where grassland was burned to enable cultivation of corn, beans, squash, and gourds.

Belmont Bog is located in a tract of 100,000 acres, 26 miles long and 6 miles wide, which was first acquired by John B. Church of New York. Settlement of the tract was slow. The region did not really flourish until the Genesee Valley Canal, an offshoot of the Erie Canal, and the Erie Railroad reached it. Owing to a lack of transportation, the lumber industry did not begin to develop until 1851, when the railroad reached Belvidere. After that, the area was extensively lumbered and burned over. Farming became important following depletion of the forests. Wheat, oats, and potatoes were the main crops, and dairy farming was very widespread. Only a few working farms are now left in the northeast section of the Town of Amity, where Belmont Bog is located.

MATERIALS AND METHODS

Belmont Bog. Field work at Belmont Bog was carried out during the summers of 1973 and 1974. The basin was probed to determine the depth and nature of sediments along an east-west transect, the longitudinal axis of the basin. Depth along the transect (see Figure 1) was tested every 10 m. by pushing a Hiller sampler to the base of the deposit. Every 50 m., a complete column of sediment was collected and examined to determine extent and unique features of the peat, gyttja, and clay. Depth across the basin was determined by three north-south transects perpendicular to the main one. One final transect was used to establish depth in the northeastern bay of the bog.

A sampling site was selected 142 m. from the western edge of the bog and 5 m. north of the east-west transect. Peat and gyttja were sampled with a Hiller borer. A Davis sampler head attached by an adapter to Lichtwardt rods (Lichtwardt, 1952) was used to sample clay. Extruded samples were wrapped in plastic film and aluminum foil and stored at low temperatures until they were subsampled in the laboratory. A screw (shipwright's) auger (4.9 cm. in diameter, 50 cm. long) attached to Lichtwardt rods was used to collect the deepest clays. This type of sampler presents problems with deformation and contamination of sediment, but it was the only means by which to penetrate the extremely compact clays at the base of the deposit. The clay, which collected in the worm of the auger, was cleaned of surface contaminants by cutting off and discarding the outermost portions.

Samples for radiocarbon dating were collected with the Davis and Hiller samplers. Owing to small diameter chambers, repetitive sampling was necessary to collect sufficient material. Sampling was confined to an area not more than 1.5 m. from the coring site. Approximately twenty peat or gyttja samples were obtained in 5 cm. lengths from each of the following depths: 0.47–0.52 m., 1.43–1.48 m., 2.47–2.52 m., 3.45–3.50 m., and 3.70–3.75 m. These were dessicated and sent to the radiocarbon

laboratory at Heidelberg University (West Germany) for analysis. Organic clay samples were submitted to the radiocarbon laboratory at the University of Wisconsin's Center for Climatic Research. Approximately forty repetitive samples, each 5 cm. in length, were collected with the Davis corer at both 4.70--4.75 m. and 5.68–5.73 m. The lowest sample contained too little organic matter for dating.

Standard methods for deflocculation, removal of siliceous materials, and acetolysis described in Faegri (1975) were used to concentrate pollen and spores present in the samples. A uniform volume of sediment from all sampled levels was processed. This was accomplished by packing sediment into a glass graduated cylinder that had been cut off to hold 1 ± 0.05 cc.

Preparatory to using the exotic pollen technique for determination of absolute pollen frequency (Matthews, 1969; see also Bonny, 1972, and Peck, 1974), residues were washed several times with water and were put into 95% ethyl alcohol. One-half or one cc. of an exotic pollen mixture was added to each residue. The exotic marker, *Zamia floridana* pollen suspended in pure glycerine, was mixed on a magnetic stirrer for at least one hour to insure homogeneity before adding it to a sample. The concentration of pollen in the suspension was determined to be $7.49 \pm 0.18 \times 10^4$ grains/cc. through a series of counts using an AO Spencer hemacytometer. One hundred counts were needed to determine the mean number of grains with a confidence level of 95% using the formula given by Bonny (1972). As suggested by Bonny (1972), the marker was added at the end of sample treatment. This is useful, because contaminants on the *Zamia* strobilus or those introduced during procedures used to extract pollen from it remain unacetolyzed and are therefore identifiable.

Residues were mounted in silicone oil (12,500 c.s.) after being suspended in tertiary butyl alcohol (TBA). Slides were heated on a warming tray (75°C) to promote evaporation of the TBA, and residues were mixed with silicone oil using a clean dissecting needle. Cover slips were sealed with nail polish once the silicone oil had spread out evenly underneath.

Only slides with a uniform distribution of pollen were used for the counts. To check if the distribution of grains was random, the slides were examined visually. Also, as suggested by Peck (1974), a Chi square test based on observed and expected frequencies of grains in successive traverses was used. Slides for which the χ^2 values were significant ($P < 0.05$) were rejected.

Three hundred arboreal pollen grains were counted at nearly all sampling depths. Counting was done at a magnification of 250×, and more difficult determinations were made at a magnification of 1000× with the use of an apochromatic oil immersion lens. Identification of pollen was aided by a small but adequate reference collection. Spear counted most samples, except for seven levels in Zone T which were tallied by Miller.

The sum was calculated by totalling the number of pollen of trees and nonarboreal plants excluding spores, pollen of bog species and other aquatics, broken pine and spruce grains, and indeterminable, badly cor-

roded or crumpled, and unknown grains. Calculation of the relative frequency of the excluded categories was done separately from the arboreal and nonarboreal pollen by using the total number of all pollen and spores in a count as the percentage base.

Absolute pollen frequency was calculated using the following formula:

$$\text{(Number of exotic pollen grains added)} \left(\frac{\text{count of fossil grains}}{\text{count of exotic grains}} \right)$$

The absolute frequency of each pollen or spore type in a count was calculated by a similar proportion. Pollen influx values, i.e. the number of grains deposited/cm.^{2}/year, were determined by dividing the absolute frequency by the number of years it took one cm. of sediment to accumulate.

Per cent organic matter in the sediment (see FIGURE 2) was measured by determining the weight of 1 cc. samples after they dried for 24 hours (at 105°C) and the weight of the ash after the samples burned for 1 hour in a muffle furnace (at 550°C). The difference between the two figures divided by the dry weight value and multiplied by 100 gives the per cent weight loss on ignition.

GENESEE VALLEY PEAT WORKS. Methods used to prepare the relative frequency pollen diagram for this site and to produce the absolute pollen frequency data, which were obtained by a somewhat different volumetric technique than that described above, are given by Miller (1973).

RESULTS

POLLEN DIAGRAMS

The Belmont Bog pollen profile (FIGURE 2) has been divided into Zones T, A, B, C-1, C-2, C-3a, and C-3b to facilitate comparison with profiles from nearby regions. Percentages of pollen types not included on the pollen diagram are given in APPENDIX C.

ZONE T (7.1–4.7 m.). Zone T consists of pollen deposited in the lower 2.4 m. of clay and shows little internal differentiation. The zone is characterized by abundant nonarboreal pollen (NAP), which varies from a high of about 70% (6.1 m.) to a low of about 50% at the end of the zone. Spectra at 5.8 and 7.1 m., containing 49 and 63% NAP respectively, were contaminated with pollen from younger sediment, presumably as the unprotected auger was pulled to the surface. Hemlock pollen accounts for 1.3% of the sum at 5.8 m., but it does not occur at sampled levels immediately above or below. At 7.1 m. only a few hemlock pollen grains were found. Additional samples were counted at 6 and 6.8 m., and although these agree well with other Zone T pollen assemblages, they were rejected because of more abundant contaminants.

The relative frequency pollen diagram (FIGURE 2) gives percentages

of major pollen types in Zone T. Cyperaceae and Gramineae are the principal NAP components. From 55 to 32% of the pollen total was contributed by members of these families. There is a general reduction upward in the amount of Cyperaceae pollen present, but the representation of Gramineae is more or less constant throughout the zone. Percentages of *Alnus* and *Salix* are also fairly constant (ca. 3–4% each). Both *Artemisia* and high-spine Compositae are somewhat better represented above 5.6 m. Pollen of *Thalictrum* is present throughout, and maximum percentages occur near the beginning and end of the zone.

The two principal arboreal pollen (AP) components are *Picea* and *Pinus*. The percentage of *Picea* pollen increases from 13% (7.1 m.) to 22% (4.8 m.). Three categories of pine pollen are shown on the diagram. The only regional species of *Pinus* subg. STROBUS is *Pinus Strobus*, and no pollen of this species was found between 7.1 and 5.6 m. except for a few grains probably present as contaminants. The body width of most pollen in the *Pinus* undifferentiated category (those grains in which the germinal furrow was obscured by grain orientation, folding, or breaking) and in the *Pinus* subg. PINUS category measure 35–40 μm. Since *Pinus Banksiana* has been found to be about this size (Whitehead, 1964), it probably is the dominant pine represented in Zone T sediments. Total *Pinus* pollen generally accounts for 16 or 17% of sums between 7.1 and 5.5 m., but from 5.5 to 4.7 m., pine comprises 10 to 13% of the total.

Low percentages of pollen from *Acer*, *Fraxinus* (4-colpate grains), *Carya*, and *Ulmus* occur sporadically throughout Zone T. Somewhat more frequent is pollen from *Quercus*, *Fraxinus* (3-colpate grains), *Betula*, and *Carpinus* or *Ostrya*.

Since the number of grains/cc. shows little variation in Zone T (FIGURE 3A), the sedimentation rate (0.062 cm./year) was probably constant during accumulation of sediments assigned to this zone (FIGURE 3C). The rate is in the same order of magnitude as that calculated for Rogers Lake, Connecticut (Davis, 1967b), but the rate at Rogers Lake is about 1.7 times greater. Total pollen influx was about 1200 grains/cm.^{2}/yr. at the base of Zone T at Belmont Bog. Above 6.2 m., pollen influx gradually increases until a maximum of 3000 grains is reached at the top of the zone. A fairly sharp change in influx (1600 to 2600 grains) occurs between 5.8 and 5.4 m.

The pollen influx diagram (FIGURE 4) yields some important additional details. Influx of Cyperaceae pollen (ca. 500 grains/cm.^{2}/yr.) remains more or less constant throughout the zone except for higher values between 5.2 and 5.4 m. Influx of Gramineae, which is about 50 grains at 7.1 m., increases gradually to 200 grains at 5.6 m. and to 350 grains at 4.8 m. Influx of *Picea* pollen is low (ca. 150 grains) until about 5.8 m. Above this level, influx increases to about 800 grains (4.7 m.). The magnitude of pine pollen influx is similar to spruce until about 5.8 m.; how-

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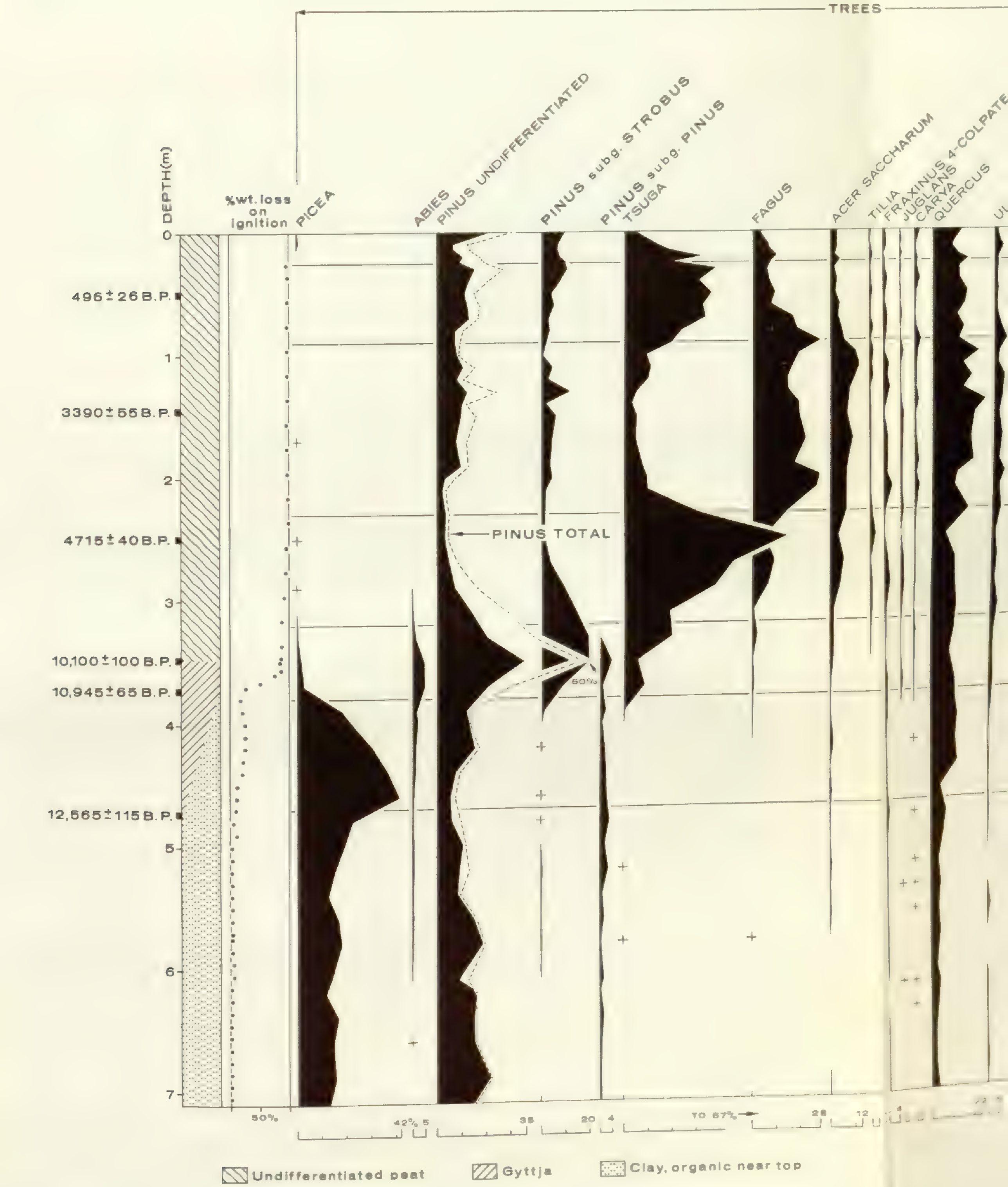
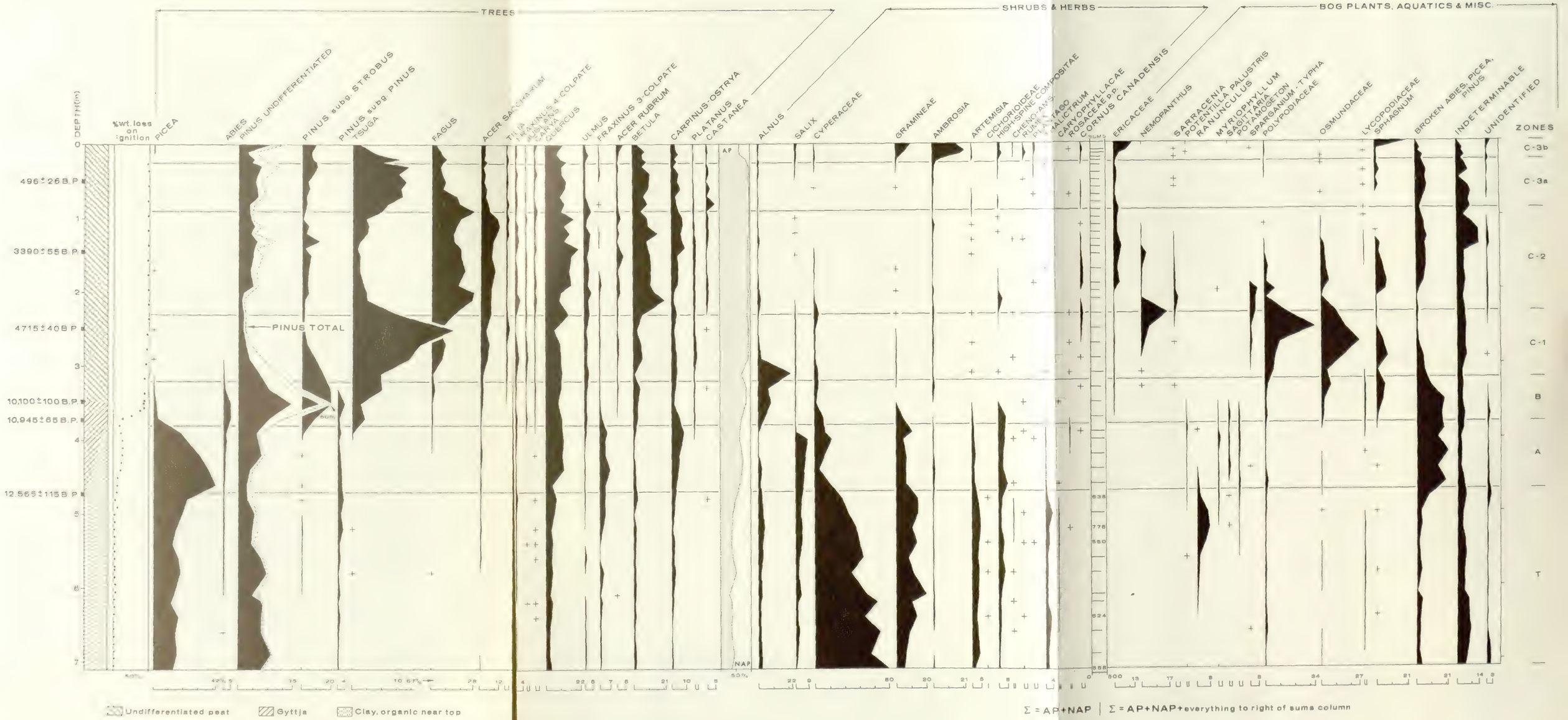
FIGURE 2. Relative pollen frequency diagram for Belmont Bog, Allegany County, New York.

BELMONT BOG, ALLEGANY COUNTY, NEW YORK: RELATIVE POLLEN FREQUENCY



BELMONT BOG ALLEGANY COUNTY, NEW YORK: RELATIVE POLLEN FREQUENCY



ever, pine influx never exceeds 300 grains/cm.^{2}/yr. in the upper portion of Zone T. Total influx of pollen from deciduous trees is never more than 250 grains at any one level throughout Zone T.

Zone A (4.7–3.8 m.). Abundant *Picea* pollen occurring in 0.9 m. of clay is found in Zone A. The T/A boundary has been placed at 4.7 m., and this level (4.7–4.75 m.) was dated at 12,565 ± 115 yrs. B.P. Spruce pollen increases from 22% (4.8 m.) to a maximum of 42% (4.6 m.) early in Zone A, then gradually decreases to 18% at the top of the zone.

Total *Pinus* pollen increases from 8% at the bottom of the zone to 23% at the top. Pollen of *Pinus Strobus* does not begin to increase until 3.9 m. Because measured pine pollen below 3.9 m. are small, *Pinus Banksiana* is probably the dominant pine represented below this level. Besides *Pinus Strobus*, pollen of *Abies*, *Tsuga*, *Fagus*, *Fraxinus* (4-colpate), and *Platanus* increase in frequency between 4 m. and the end of the zone. *Fraxinus* (3-colpate) and *Carpinus-Ostrya* increase to 5 and 7.5% respectively upward in the zone. Several tree pollen types listed above can be identified to species, since one or in some cases two species occur in the northeastern United States. They are *Abies balsamea*, *Tsuga canadensis*, *Fagus grandifolia*, *Fraxinus americana* or *F. pennsylvanica* (*Fraxinus* 4-colpate), *Platanus occidentalis*, and *Fraxinus nigra*. Pollen of *F. quadrangulata* usually has three colpi like that of *F. nigra*, but because of its southern distribution, *F. quadrangulata* can be eliminated.

NAP percentages remain high (25–35%) in Zone A. Upward in the zone sedge pollen decreases from 10%. Representation of grass pollen varies from about 10% at the bottom of the zone to 5% at 4 m. to over 12% at 3.9 m. The only other herb pollen in any abundance is from species of *Ambrosia* and *Artemisia* and from other Compositae.

Total pollen influx, based on a sedimentation rate of 0.062 cm./yr., increases from 3000 grains/cm.^{2}/yr. (4.6 m.) to 4400 grains (3.9 m.) and finally to over 6000 grains at the top of the zone. Above 3.9 m. the amount of pollen from *Pinus Strobus* and deciduous trees shows a marked increase.

The pollen influx diagram (Figure 4) adds additional details. Influx of *Picea* pollen increases from 800 grains/cm.^{2}/yr. to a maximum of 1400 grains (4.4 m.), after which it steadily declines to 300 grains at the boundary between Zones A and B. Influx of *Abies* pollen increases from $<$ 50 grains (4 m.) to 200 grains (3.8 m.). Pine has a low influx ($<$ 450 grains) until 3.9 m., where a sharp increase begins. At 3.8 m. 2000 grains were deposited/cm.^{2}/yr., and a further increase occurs above this level. Between 4.6 and 4.4 m., influx rates for *Quercus*, *Carpinus-Ostrya*, and *Salix* double, and these higher rates are maintained to the top of Zone A. At the beginning of the zone influx of Cyperaceae and Gramineae is 300 and 225 grains respectively. Both drop to a low of 120 grains within Zone A and then return to higher values at the zone A/B boundary.

ZONE B (3.8–3.2 m.). Assemblages of pine pollen characteristic of Zone B were deposited in three different types of sediment. The bottom 0.075 m. of sediment is clay. The transition from clay to gyttja occurs between 3.75 and 3.7 m. and is dated at 10,945 ± 65 yrs. B.P. (H: 4125–3279). A thin layer of gyttja (0.25 m.) accumulated over a period of about 850 years, after which the sediment changed to peat. The gyttja/peat transition (3.50–3.45 m.) has been dated at 10,100 ± 100 yrs. B.P. (H: 4125–3278). The remainder of Zone B sediment is peat.

In the relative frequency pollen diagram (FIGURE 2) all three *Pinus* curves show maximum percentages at 3.5 m. At this depth total *Pinus* is nearly 60% of the percentage base. *Pinus Strobus* accounts for at least one-third of this total and perhaps more, since some of the grains in the *Pinus* undifferentiated category are probably *Pinus Strobus*. However, the small size of many grains in *Pinus* subg. PINUS and *Pinus* undifferentiated categories indicate that *Pinus Banksiana* was also present. Spruce pollen decreases from 7% at the base of the zone to 1% at 3.5 m. and completely disappears near the B/C-1 boundary. *Abies* increases to 5% near the base of the zone and declines to 1% at the transition to Zone C-1. Percentages of deciduous tree pollen remain more or less constant during Zone B.

Between 10 and 25% of Zone B pollen sums are in the NAP category. *Alnus*, which accounts for most of the NAP, increases from 0% (at 3.8 m.) to 12.5% at 3.2 m. Cyperaceae decline from 7% (at 3.8 m.) to 2% at 3.5 m., a value that is maintained for the rest of the zone. Pollen of *Salix*, Gramineae, *Artemisia*, and various other Compositae has nearly disappeared by the middle of Zone B. Pollen of aquatic or semiaquatic plants such as *Potentilla palustris*, *Potamogeton*, *Myriophyllum*, and *Sagittaria* disappear above 3.6 m., while bog inhabitors (Ericaceae, *Nemopanthus*, and *Sarracenia*) are first detected between 3.5 and 3.3 m. Spores of species in the Polypodiaceae, Osmundaceae, and *Sphagnum* increase from < 1% to about 5%.

The number of grains/cc. (FIGURE 3A) increases by a factor of 10 from 7×10^4 to 7×10^5 (3.8–3.5 m.) and then decreases to 4.3×10^5 (3.3 m.). The sedimentation rate (see FIGURE 3C) changes three times in the zone. The deposition rate of clay is assumed to be the same as in Zones T and A. With the use of the radiocarbon dates that bracket the thin layer of gyttja, its sedimentation rate was calculated to be 0.03 cm./yr. Above 3.45 m., too few radiocarbon dates were obtained to accurately calculate a deposition rate for the peat. Hence, the pollen influx diagram (FIGURE 4) ends at 3.5 m. From 3.8 to 3.5 m., *Picea* influx decreases from 300 to 200 grains/cm.^{2}/yr. Pollen influx of both *Abies* and *Pinus* increases, *Abies* from 200 to 750 grains and *Pinus* from 2000 to 9600 grains. Influx values for *Quercus*, *Betula*, and *Alnus* also increase, while values for *Fraxinus* (3-colpate), *Carpinus-Ostrya*, Cyperaceae, and Gramineae either decline or remain constant.

For the upper 3.3 m. of sediment, an absolute frequency diagram (grains/cc.) was prepared. Although absolute pollen diagrams do not

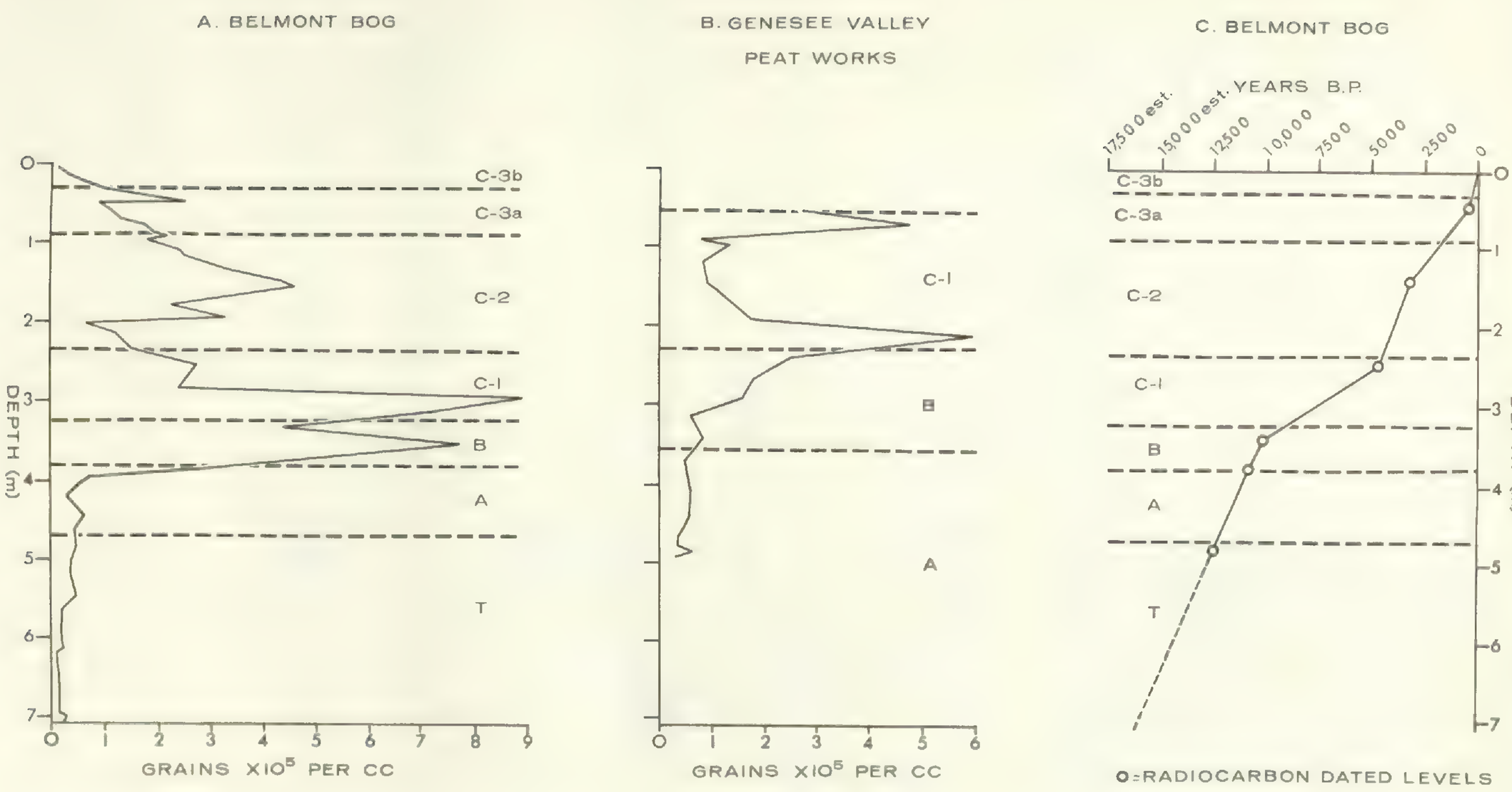


FIGURE 3. **Graphs:** A, absolute pollen frequency (grains/cc.) at Belmont Bog; B, same variable at Genesee Valley Peat Works; C, depth *versus* radiocarbon age of dated sediment samples (the sedimentation rate is the slope of the curve).

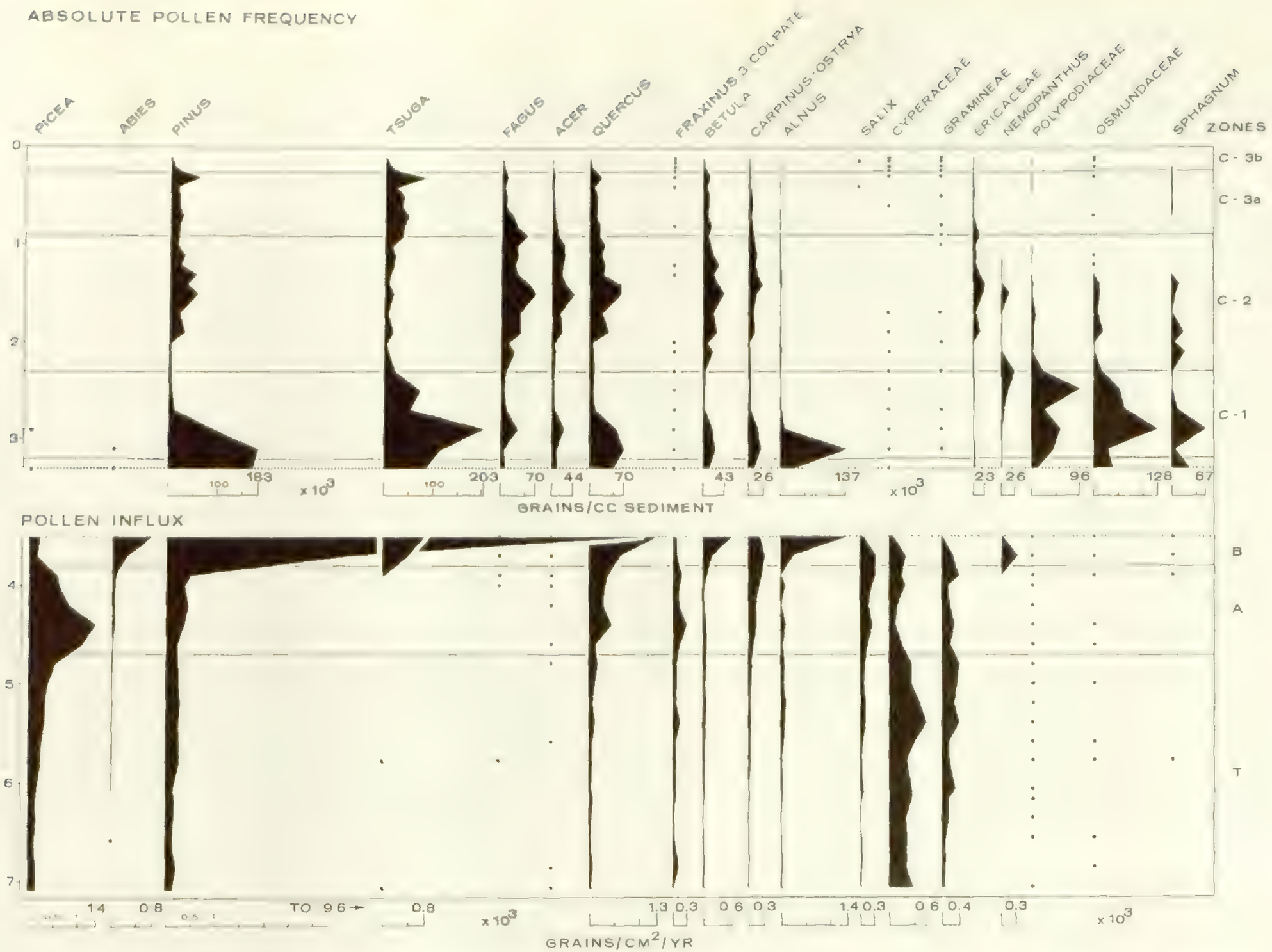


FIGURE 4. Diagrams of absolute pollen frequency (upper half) and pollen influx (lower half) at Belmont Bog.

eliminate the influence of sedimentation rate on pollen concentration, they allow the problem of interdependence of percentages to be bypassed. Too little of Zone B is shown on the absolute pollen diagram (FIGURE 4) to warrant discussion at this point.

ZONE C-1 (3.2–2.3 m.). High relative numbers of *Tsuga* pollen characterize Zone C-1, which is recorded in 0.9 m. of peat. The boundary between Zones B and C-1 (3.2 m.) was placed at the middle of the *Pinus* decline and the *Tsuga* rise. Total pine pollen decreases from 34 to $< 5\%$ upward in the zone. On the basis of size measurements and morphology, most pine pollen was contributed by *Pinus Strobus*. No pollen assignable to the *Pinus* subg. PINUS category occurs in Zone C-1, although *P. resinosa* pollen is possibly a significant proportion of the *Pinus* undifferentiated category. Hemlock pollen increases from 17% to a peak of $> 65\%$ at 2.5 m. Sediment between 2.47 and 2.52 m. was dated at 4715 $\pm$ 40 yrs. B.P. (H: 4124–3296).

Pollen of *Fagus*, *Acer*, and *Betula* increase slightly in percentage, while representation of other trees remains constant. The total percentage of NAP is low ($< 5\%$) throughout the zone, except at 3.1 m., where abundant *Alnus* pollen was recorded. Pollen and spores from known and presumed bog species fluctuate greatly in the zone. Spores of *Sphagnum* reach a maximum of 8% at 2.9 m. and gradually decrease upward. Osmundaceae rise from 5% (at 3.2 m.) to 25% at 2.7 m. and decline to 10% at the top of Zone C-1. Spores of members of the Polypodiaceae reach a maximum of $> 30\%$ at 2.5 m. *Nemopanthus* pollen, which was $< 1\%$ at 2.8 m., attains a maximum of 17% at the C-1/C-2 boundary.

The absolute number of grains/cc. (FIGURE 3A) reaches 8.9×10^5 at 2.9 m., then declines to 1.5×10^5 at the end of the zone. The absolute frequency diagram (FIGURE 4) shows some interesting trends. *Tsuga* pollen concentration increases upward in the zone, and at 2.5 m. its maximum concentration occurs. Maximum percentages of *Tsuga* also occur at this depth. However, the extent of the increase may be diminished by an increase in the sedimentation rate at the C-1/C-2 transition (see FIGURE 3C). Above 2.5 m., the absolute number of *Tsuga* pollen decreases. Spores from members of the Osmundaceae reach a maximum value at 2.9 m. and become gradually less abundant upward in Zone C-1. Both *Nemopanthus* and Polypodiaceae reach maximum numbers in the last 0.2 m. of Zone C-1 sediment.

ZONE C-2 (2.3–0.9 m.). The most significant event in Zone C-2 is the *Tsuga* decline. The C-1/C-2 boundary was placed at 2.3 m. halfway through the abrupt decrease in percentages of *Tsuga* pollen (FIGURE 2). *Tsuga* percentages remain low ($< 10\%$) until the end of Zone C-2 (0.9 m.), where an increase to 20% occurs. Near the center of Zone C-2, sediment was dated at 3390 $\pm$ 55 yrs. B.P. (H: 4123–3277). During the interval of lowest *Tsuga* frequency (2.1–1 m.), percentages of *Pinus*, *Fagus*, *Acer*, *Quercus*, and *Betula* increase. NAP percentages re-

main low throughout the zone ($< 5\%$). Percentages of pollen and spores of bog species vary considerably within the zone. Significant amounts of Ericaceae (ca. 5%) are first detected at 1.9 m. At the base of Zone C-2 *Nemopanthus* has reached 17% of the sum; however, it becomes greatly diminished upward. Both Polypodiaceae and Osmundaceae decline from high values at the beginning of the zone and then disappear near its end. *Sphagnum* increases from $< 5\%$ (2.3 m.) to 20% (2.1 m.), but it also disappears near the end of the zone. The absolute pollen diagram shows that the number of grains/cc. of *Pinus*, *Fagus*, *Acer*, *Quercus*, *Betula*, and *Carpinus-Ostrya* increase and exceed the number of grains/cc. of *Tsuga* throughout most of the zone.

ZONE C-3a (0.9–0.25 m.). Increased percentages of *Tsuga* pollen characterize Zone C-3a. The C-2/C-3a transition was placed at 0.9 m. near the midpoint of *Tsuga* increase. Within the zone *Tsuga* reaches a maximum of 37% near the C-3a/C-3b boundary. Total *Pinus* pollen increases gradually from 10% to 25%. *Fagus* decreases from 27% to 7% in the same interval. Percentages of *Acer* decrease slightly.

The number of grains/cc. undergoes considerable change (FIGURE 3A), varying from 2.2×10^5 grains (0.9 m.) to 1.0×10^5 (0.4 m.) to 2.5×10^5 grains (0.30 m.). The number of *Tsuga* grains/cc. increases from 1.2×10^4 (1 m.) to 4.6×10^4 (0.9 m.) and to 8.0×10^4 near the top of the zone. As in the relative frequency diagram, the absolute number of *Fagus* and *Acer* pollen decreases. Sediments between 0.47 and 0.42 m. gave a radiocarbon age of 496 ± 26 yrs. B.P. (H: 4122–3286).

ZONE C-3b (0.3–0 m.). This, the topmost zone of the profile, is characterized by high values for NAP categories, especially Gramineae and *Ambrosia*. Upward in the zone, Gramineae increases from 5% to 10%. In the same interval *Ambrosia* increases from about 2.5% (0.25 m.) to 25% (0.1 m.), although only 13% *Ambrosia* pollen occurs in the surface sample. A reduction of *Tsuga* representation from about 25% to 2% occurs upward in the zone. Percentages of *Fagus* and *Betula* also decline. After initial lows, *Pinus*, *Acer*, and *Quercus* show increases above 0.1 m. Two groups of bog plants markedly increase in Zone C-3b, Ericaceae from 2% (0.3 m.) to 18% (surface) and *Sphagnum* to 22% above 0.1 m.

The number of grains/cc. (FIGURE 3A) decreases from 2.5×10^5 to 2.0×10^4 upward in the zone. The absolute pollen diagram (FIGURE 4) shows decreases for all categories recognized.

SURFACE SAMPLES

To facilitate interpretation of the fossil pollen spectra, particularly Zone C assemblages, surface samples were collected from several mature, undisturbed forest stands. Three samples obtained from sites in northwestern Pennsylvania (Cook Forest, Hearts Content, and Tionesta Scenic Area) are graphed in FIGURE 5 (see also APPENDIX D). Surface and presettlement (0.3 m.) spectra from Belmont Bog are included for com-

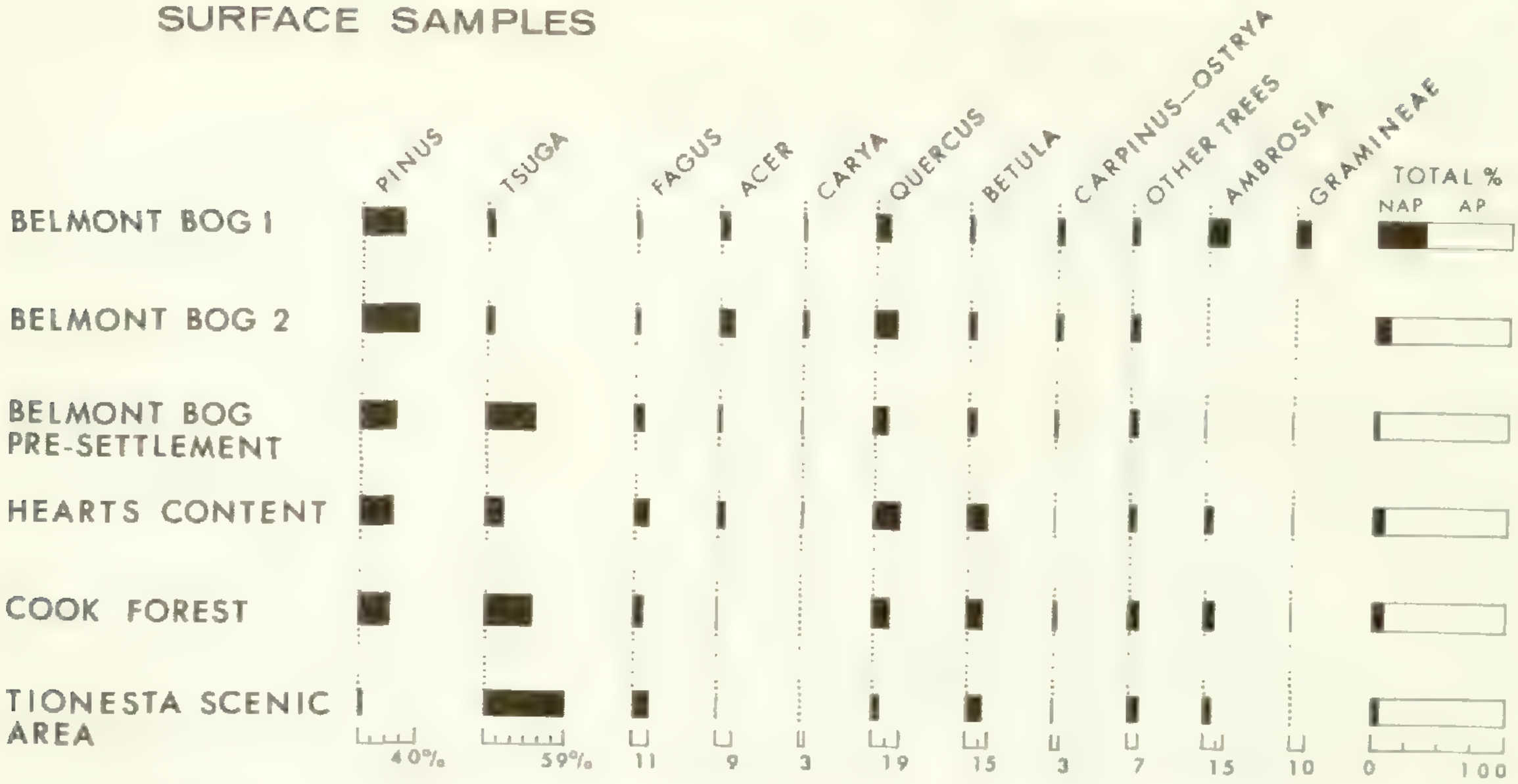


FIGURE 5. Surface pollen assemblages from sites in west-central New York State and northwestern Pennsylvania. Percentage base for Belmont Bog 1 included agricultural indicators; for Belmont Bog 2, agricultural indicators were excluded from the percentage base.

parison. The surface sample from the bog has been calculated both including (Belmont Bog 1) and excluding (Belmont Bog 2) agricultural indicators (*Ambrosia*, Chenopodiaceae-Amaranthaceae, Gramineae, *Plantago*). The most important trees in these samples are *Pinus*, *Tsuga*, *Quercus*, and *Betula*. NAP values are generally low ($< 10\%$), except for the Belmont Bog surface sample.

INTERPRETATION AND DISCUSSION

VEGETATION RECONSTRUCTION

ZONE T (16,400[2] to 12,500 yrs. B.P.). Zone T spans a period of 3900 years and is characterized by high percentages of pollen of herbs. The pollen assemblages represent an open, tundralike vegetation, but the exact nature of this vegetation, particularly the density of trees (if indeed any occurred near the depositional basin), is uncertain. Zone T pollen assemblages from Belmont Bog are in general similar to equivalent spectra at other sites in glaciated North America (Davis, 1967a), except that in the Midwest more spruce and less pine occurs, while in New England the reverse is true. Belmont Bog spectra are intermediate in this regard. Even though Zone T at Belmont Bog spans a much longer interval of time, its floristic composition is almost identical to Zone T at Allenberg Bog (Miller, 1973), which is 80 km. to the west in New York State. Zone T pollen assemblages at these sites compare well with surface pollen accumulations from the boreal forest-tundra ecotone at Fort Churchill, Manitoba (Ritchie & Lichti-Federovich, 1967). Also similar are spectra from a site 350 km. to the south in Maryland which

[2] This date is estimated assuming constant sedimentation rate (see FIGURE 3C). Estimated dates are marked with an asterisk.

show that tundra extended far southward in the Appalachians between 18,500 and 12,600 years ago (Maxwell & Davis, 1972).

Division of Zone T into two parts, one interpreted as treeless tundra with an extreme climate and the other as park-tundra with scattered trees and perhaps a warmer climate, is indicated by the pollen influx data. Between 7.1 and 5.8 m. (16,400*–14,200* yrs. B.P.), 1200 to 1600 grains/cm.^{2}/yr. were deposited. Pollen influx of this magnitude is well within the range of values given by Davis *et al.* (1973) for tundra regions. Sedges account for almost half of the influx (500 grains/cm.^{2}); *Picea* and *Pinus* each have values of 150 grains, and 50 grains of *Quercus* occur. Low influx values for these trees indicate that they probably were absent from the region around Belmont Bog early in Zone T time.

The upper park-tundra subzone (5.8–4.7 m.; 14,200*–12,500 yrs. B.P.) was deposited during retreat of ice from western New York, in particular during withdrawal from the Lake Escarpment/Valley Heads and younger moraines (see dates in Calkin, 1970). In the upper part of Zone T, pollen influx increases from 1600 to 3000 grains/cm.^{2}/yr. These values fit those available for forest-tundra vegetation with sparse stands of *Picea glauca* and *P. mariana* (Ritchie & Lichti-Federovich, 1967). Influx values for Cyperaceae and Gramineae increase slightly, and at other sites this increase in pollen production has been accounted for by a warming climate or by the increased protection offered by trees (Davis, 1969b). Influx values for *Pinus* and *Quercus* remain more or less constant in the upper part of Zone T, indicating that they were probably still absent from surfaces near the site. In contrast, influx values for spruce rise from 300 to 850 grains upward in the zone, meaning that spruce had become established in scattered stands near the basin late in Zone T time. During this period spruce seems to have migrated closer to the basin at a rate much faster than that of either pine or oak.

Based on the relative frequency diagram, Zone T at Belmont Bog shows little internal differentiation. No major fluctuations of pollen percentages are present which can be correlated conclusively with oscillations of ice fronts to the north. There is no evidence of any change in climate during the period in which Zone T sediments accumulated except for gradual warming between 16,400* and 12,500 yrs. B.P. These results support Davis and Deevey's contention (1964) that percentage fluctuations of pollen present in southern New England in zones comparable to Zone T in western New York have little relationship to vegetation change, since they involve small absolute numbers of grains. The results also agree with prespruce zone pollen profiles in Minnesota (Cushing, 1967), where no vegetation changes have been found to correlate with fluctuations of ice lobes.

ZONE A (12,500 to 11,000 yrs. B.P.). During the 1500 years represented by Zone A, vegetation adjacent to the Belmont Bog depositional basin was probably open spruce woodland. There are several pieces of evidence indicating that the vegetation was open rather than closed spruce

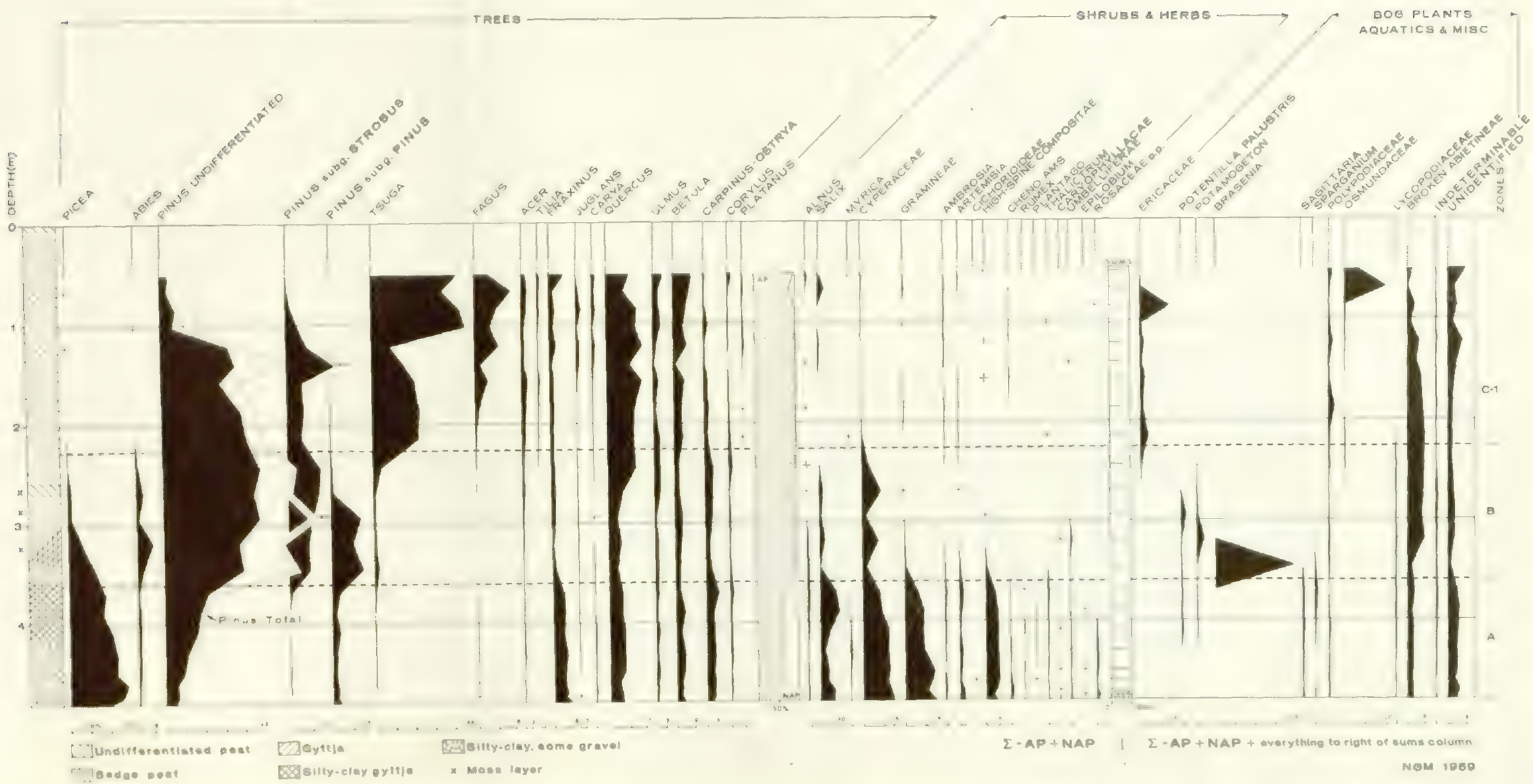


FIGURE 6. Relative pollen frequency diagram from Genesee Valley Peat Works, Allegany County, New York (modified somewhat from Miller, 1973).

forest. Percentages of spruce pollen in the zone are low (42% of the pollen sum), and NAP percentages are unusually high (25-30%). In addition, certain nonarboreal plants represented in the zone, such as *Salix* (which reaches maximum values in Zone A), *Epilobium*, *Campanula*, *Ambrosia*, Chenopodiaceae or Amaranthaceae, Caryophyllaceae, *Thalictrum*, and *Artemisia*, have high light requirements. Influx values for Gramineae and Cyperaceae are maintained at significant levels (ca. 300 grains/cm.^{2}/yr.) but are slightly reduced from values in Zone T. Total pollen influx for Zone A spectra (3000 to 6000 grains) compares well with the range of values given in Davis *et al.* (1973) for spruce woodland.

A comparable zone of low spruce and relatively high NAP percentages was found at the nearby Genesee Valley Peat Works (FIGURE 6). Miller (1973) had difficulty interpreting this zone and suggested two alternatives. One was that spruce forest existed in the uplands around the site and species contributing NAP occurred in marshes on poorly drained surfaces adjacent to the basin. If this situation prevailed, less NAP should be present at Belmont Bog, where the surrounding slopes are steep. Sampling sites close to each other but at a critical distance help separate local and regional components of the pollen rain (Turner, 1970; Brubaker, 1973), and since Zone A sediments at both sites have high percentages of NAP, local influences appear to be ruled out. Consequently, the second alternative, sparse spruce woodland, is supported by data from Belmont Bog.

Spruce is the most abundant pollen type found in Zone A. Forty-two per cent *Picea* pollen is present near the bottom of the zone, and maximum influx values (1350 grains/cm.^{2}/yr.) also occur at this level. Therefore, *Picea* should have reached its maximum density in the vegetation early in Zone A, just above sediments radiocarbon dated at 12,565 yrs. B.P. Sediments from 4.4 to 3.8 m. record a steady decline in *Picea* influx and slight increases in influx of other species. Although only the number of grains/cc. was determined for sediments from the Genesee Valley Peat Works (FIGURE 3B), these data agree closely with determinations of the same variable at Belmont Bog (FIGURE 3A). Total pollen concentration in Zone A ranges from 4.2 to 8.5 $\times$ 10^4 grains/cc. at the Peat Works and from 4.5 to 7.1 $\times$ 10^4 at Belmont Bog. The maximum number of spruce pollen/cc. at both sites is nearly the same (16,000 at the Peat Works *versus* 22,000 at Belmont Bog), and these values are reached at equivalent levels. Similar maximum concentrations of Cyperaceae pollen occur at the Peat Works (17,400) and Belmont Bog (17,200). The general correspondence of the absolute pollen data indicates regional continuity in the vegetation during Zone A time.

Influx of pine pollen remains low (ca. 400 grains) until 3.9 m. Without macrofossils it is impossible to determine if either *Pinus Banksiana* or *P. resinosa* was present or when in Zone A time pine reached the region near the depositional basin. Indeed, both pines may have occurred, even though total pine influx values are low. These pines probably do

not produce as much pollen as *P. Strobus* (Davis *et al.*, 1973); therefore, the increase in influx above 3.9 m. may relate to an abrupt appearance of *P. Strobus* at this level. Alternatively, *P. Banksiana* and *P. resinosa* could have been absent or very sparsely represented in the region until later in Zone A time (above 3.9 m.) when they increased in abundance with *Pinus Strobus*.

Higher influx values for *Quercus*, *Fraxinus*, *Carpinus-Ostrya*, and *Salix* indicate that these species either migrated closer to the depositional basin or increased in abundance as *Picea* decreased.

Zone A at Belmont Bog differs in some respects from other late-glacial profiles in eastern North America. The spruce (A) zone at Belmont is much shorter than those recorded at many New England and Midwest sites. The New England A zone has been subdivided into spruce-hardwood (12,000–10,500 yrs. B.P.) and spruce-fir (10,500–9500 yrs. B.P.) subzones. In the Great Lakes region the spruce zone can be split into spruce-hardwood (12,000–11,500 yrs. B.P.) and spruce-*Artemisia* (11,500 yrs. B.P.) subzones (Davis, 1967a). Belmont Bog has only a spruce-hardwood subzone. Spruce was abundant for only several hundred years, and it became of minor importance after 11,000 yrs. B.P. Zone A pollen assemblages at Belmont Bog compare better with similar spectra at localities south of the limit of glaciation. At sites on the New Jersey Coastal Plain, Sirkin *et al.* (1970) determined that a short spruce zone was rapidly replaced by one in which oak pollen was prominent. Martin (1958) noted the complete absence of a spruce zone in southeastern Pennsylvania and concluded that the climate went from one too cold to one too warm for spruce. In this region the vegetation changed directly from park-tundra to pine forest. Spruce-rich vegetation persisted for much less than 1500 years around the site of Belmont Bog.

The age determination at Belmont Bog for abrupt rise in spruce pollen influx, which marks the beginning of Zone A, corresponds closely with a previously reported date (12,730 ± 200 yrs. B.P.; Calkin & McAndrews, 1969) for the same event at a site in Erie County, New York, some 80 km. to the northwest.

Zone B (11,000 to ca. 8500 yrs. B.P.). The interval of time spanned by Zone B has only been approximately dated. Sediments at the bottom of the zone are about 11,000 years old on the basis of a radiocarbon date of 10,945 yrs. B.P. at 3.7 m. No date is available for the top of the zone. However, an estimate based on the sedimentation rate (Figure 3C) puts it between 9000 and 8500 yrs. B.P. The zone is characterized by a pine maximum at 3.5 m. The total influx at this depth is 2.3×10^4 grains/cm.^{2}/yr., which is low compared with modern sites in pine forest in Michigan (Davis *et al.*, 1973). Influx of this magnitude is, however, within the known range of values, and the difference may relate to the morphology of the basin at Belmont Bog.

The pine maximum at Belmont is dated at 10,100 yrs. B.P. This is

about 1000 years earlier than the pine maximum at Protection Bog (Miller, 1973), which is 70 km. to the northwest, and at Crystal Lake, 200 km. to the southwest in Pennsylvania (Walker & Hartman, 1960). The absence of synchroneity between these dates could relate to occurrence during sedimentation of ^{14}C deficient carbonate from local bedrock or till. Carbonates from such sources in limnic sediments produce age determinations that are somewhat too old. The presence of fossils of the calcicolous moss *Meesia triquetra* at equivalent levels in the basin of the Genesee Valley Peat Works (Miller, 1973) indicates that pond waters at this site, and perhaps in the basin of Belmont Bog as well, were somewhat calcareous.

Zone B at the nearby Genesee Valley Peat Works (FIGURE 6) is broader than that at Belmont Bog. However, the same time interval is probably represented, and the narrower zone at Belmont may be the result of slower sediment accumulation. Some variation in Zone B between the two sites could also be from differences in the local pollen rain. One clear difference in local pollen rain is evident. Pollen of *Alnus* is very abundant in B and lower C-1 Zone sediments at Belmont Bog, but *Alnus* pollen does not occur in Zone B at the Peat Works.

It has been speculated that the abrupt decline in spruce and subsequent rise in pine recorded at many sites in the northeastern United States was due to climatic warming, which occurred about 10,000 years ago (Ogden, 1967). However, profiles from Belmont Bog and the Genesee Valley Peat Works show a gradual decline in spruce woodland during Zone A time. An increase in pine did not occur until *Pinus Strobus* reached the area 11,000 years ago, by which time spruce abundance was greatly diminished. Hemlock also appears to have migrated into or nearer the region of Belmont Bog at the same time.

Recent research on stable isotopes in Lake Erie sediments (Fritz *et al.*, 1975), combined with results from Belmont Bog, permits the following summary of late and early postglacial events. According to Fritz *et al.* (1975), there were two periods of climatic improvement, one from 13,000 to 12.000 yrs. B.P. and the other between 10,000 and 8000 yrs. B.P. Because of its location and long sedimentary record, vegetation recorded at Belmont Bog probably reflects both of these changes. The first climatic improvement can be correlated with the transition to spruce woodland. The date for this transition at Belmont Bog (12,500 yrs. B.P.) compares favorably with an inferred date for a rise in spruce recorded in sediments of Lake Erie. However, the gradual decline in spruce beginning near the base of Zone A is more difficult to explain. Perhaps the climate warmed too fast or surfaces became edaphically unsuited for spruce regeneration and persistence. Pines and/or hemlock could not immediately replace spruce, since they did not enter the area or expand until about 11,000 yrs. B.P.

An alternative explanation for the drop in spruce influx is climatic deterioration during Zone A time. Fritz *et al.* (1975) acknowledge that after an initial increase, temperatures could have slowly dropped again

as they did in Great Britain. Unfortunately, there is an hiatus in their record between 12,500 and 10,500 yrs. B.P. caused by low water levels in an ancestral stage of Lake Erie. If a drop in temperature did occur, the region of Belmont Bog might have been more sensitive to it than lowland sites to the north because of its relatively high elevation (497 m.).

The second climatic improvement recognized by Fritz *et al.* (1975), which occurred between 10,000 and 8000 yrs. B.P., can be correlated with events in the upper part of Zone B. Maximum total pine influx, which represents the maximum abundance of pine in the vegetation, is reached at 3.5 m. (10,100 yrs. B.P.). This is just before the warming interval occurred. After the climatic change, the environment became more favorable to the development of vegetation with abundant hemlock. Further research, including more radiocarbon dated profiles north and south of Belmont Bog, is needed before details of the shift from pine to hemlock domination can be established.

ZONE C-1 (8500 to 4400 yrs. B.P.). Forests dominated by *Tsuga canadensis* are recorded in the sediments of this zone. After 8500 yrs. B.P., the climate of western New York appears to have become more uniform, and vegetation changes appear synchronous. Miller (1973) has described the nature of this zone in detail, and results from Belmont Bog support his conclusions. A pollen assemblage (FIGURE 5) from a surface sample collected in the Tionesta Scenic Area, Allegheny National Forest (McKean County, Pennsylvania) matches well most Zone C-1 pollen spectra. This indicates close correspondence between the existing vegetation of the Tionesta area and that present during Zone C-1 time near Belmont Bog. The average basal area/acre of trees in the virgin forest along East Tionesta Creek (Hough, 1936) is about 140 ft.^{2}/acre, of which 63% is *Tsuga canadensis*, 20% is *Fagus grandifolia*, and 4% is *Acer saccharum*. The remaining 3% is *Acer rubrum*, *Betula lenta*, *Betula lutea*, and *Prunus serotina*. The two dominants, *Tsuga canadensis* and *Fagus grandifolia*, occur not only on middle and lower slopes but also on plateaus.

Events in the development of the peat deposit in the basin are recorded in sediments included in Zone C-1 and the transition to Zone C-2. Since only the lower portion of Zone C-1 occurs at the Genesee Valley Peat Works (FIGURE 6), the regional significance of events above this level can not be determined. It is interesting that just before the record ends at the Peat Works, maximum percentages of Osmundaceae occur. At a comparable level Belmont Bog has a similar peak of *Osmunda* spores, followed by peaks in curves for Polypodiaceae and *Nemopanthus* higher in Zone C-1. Pollen preserved in sediments recording the transition from Zone C-1 to Zone C-2 is badly corroded. Also, there is a high in the absolute pollen frequency curve (FIGURE 3A) near the transition. This evidence indicates that the water table of the bog may have dropped (as a response to drought?), allowing peat to become oxidized. As the mat dried out, ferns (Osmundaceae and Polypodiaceae) and shrubs (*Nemopanthus*) invaded it. These categories are also included in the absolute

pollen frequency diagram (FIGURE 4), which shows the magnitude of their representation at the C-1/C-2 transition. At the beginning of Zone C-2, return to a higher water table is indicated by increases in *Sphagnum* and *Typha* and a decrease in the absolute number of grains/cc., implying a faster sedimentation rate.

It is tempting to correlate this reconstruction of bog development with the abrupt decline of hemlock at about 4400 yrs. B.P. Miller (1973) suggested that the decline could be due to several years of severe drought. However, the drought may not have been intense and of short duration, but rather a gradual drying, as is indicated by the behavior of bog plants in the Belmont pollen record. Hemlock populations weakened by such droughts may also have been adversely affected by a normally innocuous biotic agent, such as some insect or fungus.

ZONE C-2 (ca. 4400 to ca. 1700 yrs. B.P.). Low percentages of hemlock pollen are recorded in the 2700 years represented by Zone C-2 at Belmont Bog. After the abrupt decline of hemlock, succession occurred, and *Fagus grandifolia*, *Betula*, *Acer saccharum*, and *Quercus* became more abundant. These results correlate well with those of Miller (1973) and indicate that postglacial vegetation change was synchronous in western New York.

ZONE C-3a (ca. 1700 to ca. 175 yrs. B.P.). Approximately 1700 years ago, hemlock began to regain its former dominance in the forest. The increase in *Tsuga* pollen is accompanied by decreases in percentages of *Fagus* and *Acer* pollen. The bottom of Zone C-3a is marked by a small but significant increase in *Castanea* pollen. *Castanea* increases in Zone C-3 at Rogers Lake, Connecticut (Davis, 1969a), but in western New York large percentages of chestnut pollen have been detected only at Allenberg Bog (Miller, 1973). In southwestern New York during Zone C-3a, the abundance of chestnut increased, probably on south-facing slopes, a preferred habitat in presettlement forests.

A modern analogue of vegetation recorded at Belmont Bog prior to settlement by European man is Cook Forest, a state park in Clarion County, Pennsylvania, about 30 km. south of the Tionesta Scenic Area. Most of the basal area at Cook Forest (62%) is even-aged white pine which began after fire 320 years ago. Only a few white pines older than this were found (Hough & Forbes, 1943). Hemlock accounts for 36% of the basal area (Morey, 1936). Forest surrounding Belmont Bog before settlement probably contained a similar stand of white pine.

ZONE C-3b (175 calendar yrs. B.P. to present). The upper 0.25 m. of peat contains postsettlement spectra. This zone is characterized by increased percentages of NAP taxa, particularly *Ambrosia* and Gramineae.

The resolution of the profile in Zone C-3b is not good enough to show clearly events of settlement. However, a few historical trends can be detected. The lumbering and clearing of land for agriculture caused a

sharp decline in AP percentages from 0.25 to 0.10 m. Above 0.1 m., percentages of *Tsuga*, *Fagus*, and *Betula* continue to decrease, while *Pinus*, *Acer*, and *Quercus* increase. This is possibly due to the cutting of second growth stands and virgin timber.

Increasing percentages of *Pinus*, *Acer* (mostly *Acer rubrum*), and *Quercus* are probably due to forest succession, which occurred as more farmland in the region was abandoned. A decrease in *Ambrosia* between 0.1 m. and the surface also indicates a decrease in open areas with abundant weeds and an associated increase in forested land.

Evidence for the great importance of hemlock in the Zone C-3 and C-1 forests is provided by the surface pollen assemblage. Although hemlock accounts for only 2% of total pollen in the surface sample, hemlock is the second most important species (after white pine) in the forest around the bog and the second most important species on the north-facing slope. Hemlock pollen is somewhat overrepresented in the pollen record (Davis & Goodlett, 1960; Miller, 1973), so perhaps sites used for vegetation analysis were atypical for the region which contributes pollen to the Belmont Bog sedimentary basin. Nevertheless, hemlock must have been much more abundant, possibly occurring in almost pure stands, around Belmont Bog in the past.

Age of the Olean Drift

The oldest radiocarbon age of sediment in the basin is 12,565 ± 115 yrs. B.P. With the use of this date and the date immediately above, both of which are of organic matter in clay, the sedimentation rate was calculated to be 0.062 cm./yr. It is probable that sediment below 4.75 m. accumulated at a similar rate, because pollen influx was more or less constant during Zone T. This assumption having been accepted, the deepest sediments are about 16,400 radiocarbon years old. Since most workers consider the Olean drift to have been deposited in the early or middle Wisconsinan, a date of 16,400 yrs. B.P. seems much too young.

The reason older sediments were not found in the Belmont Bog basin is uncertain. The basin may in fact not be on Olean till but on younger drift perhaps of Kent age (23,000–17,000 yrs. B.P.). Terminal moraines in southwestern New York are not like the well-defined moraines of the Midwest, and consequently Kent ice perhaps advanced farther than the position thought to mark its maximum extent. Although we have not attempted to trace the Kent terminal moraine, it occurs within 4.8 km. of the site (Muller, 1957), and an error in mapping would be relatively small.

A second possibility is that the basin is actually situated on drift of Olean age and the truncated record is due to failure to collect all the sediment. Since the basin is close to the Kent margin, coarse outwash could have been deposited in it. The auger used for sampling may have been stopped by cobbles of outwash sediment.

A third alternative is that the ice block left by Olean ice did not melt

immediately. The climate was perhaps so severe that melting did not start until the onset of warming associated with the Erie Interstade. Lake deposits in Minnesota show a lag between ice retreat and the beginning of deposition (Florin & Wright, 1969). Unlike Belmont Bog, however, such deposits characteristically have a layer of coarse plant debris directly above till and below lacustrine sediment. The organic debris represents material deposited on the surface of the buried ice block before it melted.

SUMMARY

1. Pollen recovered from a 7.1 m. sediment column from Belmont Bog shows regional changes in late-glacial and postglacial vegetation when compared with the pollen record from the nearby Genesee Valley Peat Works. These sites are located in the Allegheny Plateau section of southwestern New York State, 40 km. inside the southern limit of Wisconsinan glaciation. The depositional basin is on a surface generally considered to have been deposited by Olean ice. The age of the Olean drift is unknown but is thought to be early or middle Wisconsinan.

2. Before European settlement, much of the region around Belmont Bog was covered with Hemlock-white pine-northern hardwood forest, stands of which graded into Oak-chestnut forest that occupied dry, exposed, south-facing slopes. Today, nearly all of the forest has been cut over. Northern hardwood and Oak second-growth forests are found adjacent to the bog.

3. Seven zones (T, A, B, C-1, C-2, C-3a, C-3b) were recognized in the pollen record. The lowest, Zone T, represents about 3900 years of tundralike vegetation. Based on pollen influx data, the zone can be divided into two parts, treeless tundra with perhaps an extreme climate (16,400–14,200 yrs. B.P.) and park-tundra with a slightly warmer climate (14,200–12,500 yrs. B.P.).

4. The base of Zone A was dated at 12,565 ± 115 yrs. B.P., which correlates with a warming period proposed for that time by Fritz *et al.* (1975). Early in Zone A time, open spruce woodland surrounded the depositional basin. Spruce pollen, which was never too abundant (generally < 30%), reached maximum values early in the zone. Percentages of NAP remained high throughout the interval, indicating that open conditions persisted.

5. The interval of time spanned by Zone B has not been determined directly. The bottom of the zone was dated 10,945 ± 65 yrs. B.P., and based on the sedimentation rate, Zone B ended an estimated 8500 radiocarbon years ago. The pine maximum was dated at 10,100 ± 100 yrs. B.P., which is approximately 1000 years earlier than the pine maximum at Protection Bog, a site 70 km. to the northwest. The second warming interval of Fritz *et al.* (1975) occurred during the upper part of Zone B and could account for the transition from a forest rich in pines to one with abundant hemlock.

6. Zones C-1, C-2, C-3a, and C-3b are similar to those previously described for sites in western New York. Surface samples from virgin forests in northwestern Pennsylvania match spectra in Zones C-1 and C-3a. Sediments just below the Zone C-1/C-2 transition (the hemlock decline) are 4715 ± 40 yrs. B.P. A date for the middle of Zone C-2 is 3390 ± 55 yrs. B.P. A date of 496 ± 26 yrs. B.P. from Zone C-3a was obtained at 0.47–0.52 m.

7. Assuming a fairly uniform sedimentation rate for the basal clay in the basin, the bottom of the deposit is estimated to be 16,400 years old. This is much younger than the previously inferred age of the Olean advance. Possible explanations for this discrepancy are (1) that the bog is not on Olean drift but on younger Kent till, (2) that deposition was delayed some thousands of years, or (3) that outwash from the Kent advance was deposited over pre-Kent sediment.

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APPENDIX A

Analyses of Vegetation Near Belmont Bog

Species	No.	Points of occurrence	Relative density	Relative frequency	Relative dominance	Importance value index
North-facing slope of Phillips Creek Valley						
Acer saccharum	25	13	20.8	15.8	21.5	58.1
Tsuga canadensis	25	11	20.8	13.6	19.5	53.9
Fraxinus americana	16	11	13.3	13.6	14.5	41.4
Acer rubrum	11	10	9.2	12.1	8.4	29.7
Fagus grandifolia	9	7	7.5	8.4	7.2	23.1
Quercus rubra var. *borealis*	7	6	5.8	7.3	8.5	21.6
Betula lutea	7	6	5.8	7.3	2.6	15.7
Carya ovata	5	5	4.2	6.2	4.3	14.7
Ostrya virginiana	5	5	4.2	6.2	2.0	12.4
Tilia americana	3	3	2.5	3.7	3.6	9.8
Prunus serotina	2	2	1.7	2.6	5.2	9.5
Pinus resinosa	3	1	2.5	1.1	1.0	4.6
Populus tremuloides	1	1	0.8	1.1	1.4	3.3
Carpinus caroliniana	1	1	0.8	1.1	0.3	2.2
South-facing slope of Phillips Creek Valley						
Quercus alba	33	17	27.5	22.6	34.0	84.1
Quercus rubra var. *borealis*	23	15	19.2	19.8	28.6	67.6
Acer saccharum	21	14	17.5	18.7	14.5	50.7
Fraxinus americana	16	12	13.3	15.9	8.9	38.1
Carya ovata	10	5	8.3	6.7	5.3	20.3
Populus tremuloides	6	4	5.0	5.2	3.1	13.1
Acer rubrum	3	3	2.5	4.0	1.4	7.9
Fagus grandifolia	4	2	3.3	2.4	2.0	7.7
Ostrya virginiana	2	2	1.7	2.4	0.9	5.0
Populus grandidentata	1	1	0.8	1.2	0.6	2.6
Tilia americana	1	1	0.8	1.2	0.5	2.5
Forest communities immediately adjacent to Belmont Bog						
Pinus Strobus	59	24	29.5	19.1	31.7	80.3
Tsuga canadensis	42	24	21.0	19.0	25.7	65.7
Acer rubrum	32	32	16.0	25.4	15.1	56.5
Acer saccharum	24	12	12.0	9.5	11.1	32.6
Prunus serotina	15	11	7.5	8.7	5.8	22.0
Fagus grandifolia	9	7	4.5	5.6	5.7	15.8
Betula lutea	6	4	3.0	3.2	0.9	7.1
Quercus rubra var. *borealis*	4	3	2.0	2.4	1.8	6.2
Amelanchier laevis	3	3	1.5	2.4	0.5	4.4
Populus tremuloides	2	2	1.0	1.6	0.8	3.4
Pinus resinosa	2	2	1.0	1.6	0.4	3.0
Ostrya virginiana	1	1	0.5	0.8	0.4	1.7
Betula lenta	1	1	0.5	0.8	0.2	1.5

APPENDIX B

FLORA OF BELMONT BOG AND SURROUNDING AREA *

Bog Mat

TREES:
Pinus Strobus **

SHRUBS:
Chamaedaphne calyculata
Pyrus floribunda

HERBS:
Eriophorum virginicum
Sarracenia purpurea
Vaccinium Oxycoccos

Bog Margin

TREES:
Amelanchier arborea
A. laevis

SHRUBS:
Cornus racemosa
Ilex verticillata
Lonicera Morrowii
Nemopanthus mucronata
Rhododendron roseum
Vaccinium atrococcum
Vaccinium angustifolium var. *hypolasium*
Viburnum cassinoides
V. acerifolium

HERBS:
Calla palustris
Lemna minor
Osmunda cinnamomea **

Northern Hardwood

TREES:
Acer rubrum
A. saccharum **
Betula lenta
B. lutea
Fagus grandifolia **
Fraxinus americana
Ostrya virginiana
Prunus serotina
Quercus rubra var. *borealis*
Tsuga canadensis

HERBS:
Caltha palustris
Carex gracillima
Coptis groenlandica
Cornus canadensis
Dryopteris noveboracensis
D. spinulosa var. *intermedia*
Epifagus virginiana
Lycopodium annotinum
L. clavatum
L. complanatum var. *flabelliforme*
L. obscurum
Maianthemum canadense
Mitchella repens
Oxalis montana
Polygonatum pubescens
Trientalis borealis
Trillium grandiflorum
T. undulatum

Hemlock Unit

TREES:
Acer rubrum
Betula lutea
Fagus grandifolia **
Tsuga canadensis

HERBS:
Epifagus virginiana

White Pine Unit

TREES:
Acer rubrum

* Names after Fernald (1950).

** Voucher specimen unavailable; vouchers for other plants deposited in the University of North Carolina Herbarium (NCU).

Fraxinus pennsylvanica var. *subintegerrima*
Pinus Strobus **
Populus tremuloides
Prunus serotina
Quercus rubra var. *borealis*

SHRUBS:
Vaccinium myrtilloides

HERBS:
Clintonia borealis
Cypripedium acaule
Pteridium aquilinum var. *latiusculum*

Planted Species
Picea rubens
Pinus resinosa

APPENDIX C

PERCENTAGES OF POLLEN AND SPORES FROM BELMONT BOG SEDIMENTS NOT INCLUDED IN POLLEN DIAGRAM

Nyssa sylvatica: 0.2% (0 cm.), 0.8% (14 cm.), 0.3% (20 cm.), 0.3% (24 cm.), 0.3% (60 cm.), 1.5% (80 cm.), 1.0% (90 cm.), 0.9% (110 cm.), 0.6% (120 cm.), 0.9% (130 cm.), 0.6% (140 cm.), 0.9% (170 cm.), 0.3% (190 cm.), 1.6% (200 cm.), 0.3% (210 cm.), 0.6% (230 cm.), 0.3% (270 cm.), 0.6% (290 cm.).
Prunus serotina: 0.2% (0 cm.).
Liquidambar styraciflua: 0.3% (30 cm.), 0.3% (60 cm.), 0.3% (70 cm.), 0.3% (330 cm.).
Populus: 0.4% (0 cm.), 1.5% (10 cm.), 0.8% (14 cm.), 2.3% (20 cm.), 0.9% (40 cm.), 0.6% (70 cm.), 0.3% (80 cm.), 0.6% (90 cm.), 0.6% (110 cm.), 0.6% (120 cm.), 0.6% (140 cm.), 0.6% (170 cm.), 0.9% (190 cm.), 1.6% (200 cm.), 0.3% (210 cm.), 0.6% (230 cm.), 0.3% (270 cm.), 0.2% (370 cm.).
Celtis: 0.2% (400 cm.), 0.2% (460 cm.).
Morus: 0.2% (0 cm.).
Corylus: 0.4% (10 cm.), 0.4% (14 cm.), 0.3% (24 cm.), 0.3% (50 cm.), 0.3% (60 cm.), 0.3% (70 cm.), 0.3% (120 cm.), 0.6% (130 cm.), 1.2% (170 cm.), 0.6% (190 cm.), 0.3% (200 cm.), 0.3% (210 cm.), 0.6% (270 cm.), 0.9% (330 cm.), 0.5% (350 cm.), 0.5% (370 cm.), 0.8% (390 cm.), 0.4% (400 cm.), 0.5% (420 cm.), 0.2% (440 cm.), 0.6% (460 cm.), 0.2% (480 cm.), 0.2% (500 cm.), 0.6% (540 cm.), 0.2% (560 cm.), 0.8% (580 cm.), 0.2% (620 cm.).
Myrica: 0.3% (60 cm.), 0.3% (70 cm.), 1.9% (150 cm.), 0.4% (390 cm.), 0.2% (400 cm.), 0.2% (710 cm.).
Cephalanthus occidentalis: 7.4% (0 cm.), 0.4% (14 cm.), 0.3% (290 cm.), 0.2% (370 cm.).
* ***Ilex***: 0.2% (480 cm.).
Rhamnus: 0.3% (140 cm.).
Viburnum: 0.3% (70 cm.), 0.3% (130 cm.), 1.9% (140 cm.), 1.2% (170 cm.), 3.2% (190 cm.), 1.6% (310 cm.).
* *Sambucus*: 0.3% (40 cm.), 0.3% (200 cm.).
Vitis: 0.2% (14 cm.).
Campanula: 0.2% (420 cm.), 0.2% (560 cm.).
Epilobium: 0.6% (460 cm.), 0.3% (580 cm.).

* Identification probable.

Galium: 0.3% (250 cm.), 0.2% (610 cm.), 0.2% (710 cm.).
Gentiana: 0.2% (370 cm.), 0.2% (400 cm.).
Humulus Lupulus: 0.3% (60 cm.).
Labiatae: 0.3% (200 cm.), 0.5% (370 cm.), 0.2% (400 cm.), 0.2% (460 cm.), 0.2% (540 cm.).
Polygonum: 0.3% (330 cm.), 0.3% (350 cm.), 0.4% (400 cm.), 0.3% (520 cm.), 0.2% (560 cm.).
Sanguisorba: 0.2% (400 cm.), 0.2% (500 cm.), 0.4% (520 cm.).
Saxifraga: 0.2% (480 cm.), 0.2% (560 cm.).
Shepherdia canadensis: 0.6% (390 cm.), 0.2% (480 cm.), 0.2% (500 cm.), 0.1% (520 cm.).
Umbelliferae: 0.2% (14 cm.), 0.5% (370 cm.), 0.5% (440 cm.), 0.2% (460 cm.), 0.2% (640 cm.).
Urtica: 0.6% (400 cm.).
Caltha palustris: 0.2% (0 cm.).
Utricularia: 0.2% (420 cm.), 0.2% (460 cm.), 0.2% (580 cm.).
Botrychium: 0.1% (390 cm.), 0.1% (520 cm.).
Selaginella selaginoides: 0.1% (480 cm.).

APPENDIX D

SURFACE POLLEN ASSEMBLAGES FROM BELMONT BOG AND SITES IN NORTHWESTERN PENNSYLVANIA

	BELMONT BOG 1	HEARTS CONTENT	COOK FOREST	TIONESTA SCENIC AREA
Trees, shrubs, herbs *				
Picea	0.2†	—	—	—
Pinus undifferentiated	20.7	11.4	13.7	2.6
P. subg. STROBUS	9.6	12.9	8.7	0.2
Tsuga	4.4	13.8	36.6	59.5
Fagus	2.4	10.0	5.6	10.9
Acer saccharum	2.7	1.8	—	0.6
Tilia	0.4	—	—	—
Fraxinus 4-colpate	1.1	1.5	0.4	0.8
Carya	2.0	1.8	—	—
Quercus	11.8	19.0	11.2	4.5
Ulmus	1.1	0.3	0.2	—
Acer rubrum	4.4	2.9	0.9	3.0
Betula	3.1	14.9	11.7	11.8
Carpinus-Ostrya	2.4	—	—	0.2
Platanus	0.7	0.5	2.5	—
Castanea	0.2	—	—	—
Populus	0.4	—	—	—
Nyssa	0.2	—	—	—
Prunus serotina	0.2	0.3	—	—
Morus	0.2	—	—	—
Liquidambar	—	—	0.2	—
Almus	0.9	—	0.4	0.8
Salix	1.6	—	—	—

APPENDIX D

Surface Pollen Assemblages from Belmont Bog and Sites in Northwestern Pennsylvania (*continued*)

	Belmont Bog 1	Hearts Content	Cook Forest	Tionesta Scenic Area
Myrica	—	0.3	—	—
Gramineae	10.0	0.6	0.4	—
Ambrosia	15.6	5.3	7.4	4.3
High-spine Compositae	1.6	0.3	—	0.8
Cheno-Ams.	0.7	—	—	0.2
Plantago	1.1	0.3	—	—
Thalictrum	0.2	—	—	—
Other Rosaceae	—	—	0.2	—
Umbelliferae	—	0.9	—	—
Gentiana	—	0.3	—	—
sum AP	68.4	91.2	91.7	94.0
sum NAP	31.6	8.8	8.3	6.0
Misc.**				
Ericaceae	13.0	—	—	—
Nemopanthus	0.2	—	—	—
Cephalanthus	7.4	—	—	—
Potentilla palustris	0.8	—	—	—
Sagittaria	0.5	—	—	—
Caltha palustris	0.2	—	—	—
Polypodiaceae	0.3	1.7	19.3	3.0
Lycopodiaceae	0.8	—	0.4	0.4
Osmundaceae	0.2	—	—	—
Sphagnum	21.9	—	—	—
Broken Abietineae	2.3	—	—	—
Indeterminable	2.7	—	—	3.3

* Percentage base = sum AP + NAP.
** Percentage base = sum AP + NAP + sum Misc.
† Numbers indicate percentages.

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COVER: A "mass collection" of leaves of *Sassafras albidum* (Nutt.) C. G. Nees, a handsome lauraceous tree of eastern North America and a probable Arcto-Tertiary relict, along with its two living congeners in eastern Asia. Its attractive small, yellow flowers are produced early in the spring as the leaves first unfold. The elliptic leaves, either entire, mitten-shaped, or 3-lobed at apex, become beautifully red-and-yellow colored in autumn. Although sassafras has long been thought to have medicinal properties, it is probably no more than a mild aromatic stimulant. A tea is made from the wood of sassafras roots; from its leaves, which contain ethereal oil and mucilage cells, gumbo filé, a powder used to give flavor and consistency to gumbo soup, is prepared.

Karen S. Valmure, whose original illustrations were used on the two preceding covers, also planned and executed this one, as well as the designs and devices in other parts of the Journal and on the offprint covers.

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STUDIES OF PACIFIC ISLAND PLANTS, XXXIII. THE GENUS ASCARINA (CHLORANTHACEAE) IN THE SOUTHERN PACIFIC *

ALBERT C. SMITH

THE FAMILY Chloranthaceae (Swamy, 1953b) is of exceptional interest for the primitive characteristics of its xylem, which ranges from the vesselless condition demonstrated by *Sarcandra* (Swamy & Bailey, 1950) to a low level of specialization in *Chloranthus*, *Ascarina*, *Ascarinopsis* (Humbert & Capuron, 1955), and *Hedyosmum*. The nodal anatomy of some genera of the family cannot be assigned either to a strictly unilacunar type or to a typically trilacunar one, and the pollen grains show trends of aperture type from sulcate to inaperturate to polycolpate (Walker, 1974). Reproductive structures within the family are highly reduced and therefore phylogenetically advanced in comparison to those of many other ranalean families. The component genera are morphologically sharply separable and usually have discrete ranges. One may assume that the Chloranthaceae are today represented by isolated remnants of a once diverse, widespread, and ancient assemblage of angiosperms, in which extinction has played a major role in narrowing the diversity of the few surviving representatives. The family is often ordinally assigned to either the Piperales or the Laurales, but its range of characters, some of which are extremely primitive even for those orders, together with its wide distribution and the discreteness of its surviving genera, suggests that it is best assigned to its own order Chloranthales. I would now prefer this modification of my previous assignment of the family to the Laurales, suborder Monimiineae (Smith, 1972). Walker (1976) has also pointed out the isolation of the family by recognizing it as the sole component of the suborder Chloranthineae of the order Piperales.

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Ascarina J. R. & G. Forster

My present concern with the Chloranthaceae stems from a need to clarify the nomenclature of taxa of *Ascarina* occurring in the Fijian Region. Dr. W. R. Sykes, of the Department of Scientific and Industrial Research, Christchurch, has kindly called to my attention the fact that the mid-Pacific species extending from the Solomon Islands to at least the Cook Islands was incorrectly assigned by Swamy (1953a) to *A. lanceolata* Hooker f. While investigating this situation I observed other aspects of Swamy's treatment which require adjustment, useful as it is in its major features.

(1) Swamy, like earlier students of *Ascarina*, described the genus as dioecious. While in general this is certainly the case, the occurrence of monoecy must be pointed out in at least two specimens collected in the New Hebrides. One of these, *Kajewski 152*, assigned by Swamy to *A. lanceolata* var. *smithii* (herein placed in *A. swamyana*), bears ♂ and ♀ inflorescences; however, these inflorescences occur on separated branchlets and therefore it is possible (although unlikely) that Kajewski's material came from two different plants. The second specimen, *Bernardi 12913* (not available to Swamy and herein placed in *A. diffusa*), bears ♂ and ♀ inflorescences on the same branchlet, and therefore the occurrence of monoecy is unquestionable and should be noted by future students of the genus.

(2) Swamy noted that the seven species recognized by him fall into two groups, one a predominantly western Pacific group with a single flower-subtending bract and a ♂ flower with two stamens, the other a predominantly eastern Pacific group with three flower-subtending bracts (two of which may be considered as lateral bracteoles) and a ♂ flower with a single stamen. The two groups are said to overlap only in the Solomon Islands and New Caledonia. However, Swamy failed to note that a Marquesan specimen, *Quayle 1319* (which he cited as *A. lanceolata*), falls into his "western" group and therefore minimizes the significance of the assumed geographic segregation. In the present treatment I consider the Marquesan element to represent a new species, *A. marquesensis*.

(3) The only really egregious flaw in Swamy's treatment is his failure to typify correctly *A. lanceolata* Hooker f., the holotype of which was seen by him and listed without recognition as *A. lucida* Hooker f. This holotype, *MacGillivray 982*, comes from the Kermadec Islands. Unaccountably Swamy designated a Rarotongan specimen, *Parks 22521*, as a topotype of *A. lanceolata*, to which he assigned a range extending from the Solomon Islands to the Societies and Marquesas. Since *A. lanceolata* is now seen to be a Kermadec Island endemic (whether as a species or a variety), the more widespread tropical Pacific species is left without a name unless one interprets it to include the Raiatean *A. subfalcata* J. W. Moore, as Swamy did.

(4) In fact, however, reexamination of the holotype of *A. subfalcata*

indicates it to be specifically distinct from the comparatively frequent species extending from the Solomons to the Cook Islands. The latter taxon I am herein interpreting as a new species, *A. diffusa*.

(5) The modifications here suggested increase *Ascarina* in size from seven to eleven species. Although I have studied only the tropical Pacific species in detail, I believe that at present it is desirable to avoid the use of trinomials in *Ascarina*, which merits a much more detailed review. Nomenclatural changes herein proposed include (a) establishment of the Marquesan taxon as a distinct species, (b) reestablishment of *A. subfalcata* as an endemic species from Raiatea, (c) description as a new species of a comparatively widespread Pacific taxon occurring from the Solomons to Rarotonga, (d) elevation to specific level of *A. "lanceolata"* var. *smithii* Swamy under the name *A. swamyana*, and (e) reestablishment of *A. lanceolata* as a Kermadec Island endemic species distinct from the New Zealand *A. lucida*. I herewith suggest modifications of Swamy's key to species and append comments on nomenclature, typification, and distribution, although only the species that affect my interpretation of those of the Fijian Region are treated in detail.

Key to species

Flowers subtended by a single bract (lateral bracteoles rarely present); ♂ flowers with two collateral stamens (rarely with a third, partially developed, adaxial stamen); endocarp (as far as known) comparatively smooth.

Inflorescences with congested flowers or fruits, the branches (or simple spikes of axillary inflorescences) 0.5–2 cm. long, the flowers or fruits essentially contiguous, rarely separated on the rachis by more than 2 mm.

Leaf blades elliptic to oblong, 3.2–14 × 1.5–8.5 cm., about twice as long as broad; branches of the terminal compound spike several, usually spreading from a central axis; flower-subtending bracts ovate, sometimes to 1.5 mm. long; lateral bracteoles absent; anthers about 3 mm. long and 1–1.5 mm. broad, subacuminate at apex by a projecting connective; Philippines, Borneo, and New Guinea. . . . . 1. *A. philippinensis*.

Leaf blades lanceolate to narrowly elliptic, 3.5–9 × 1–4 cm., more than twice as long as broad; branches of the central axis of the terminal compound spike 1 or 2, subascending; flower-subtending bracts broadly deltoid to reniform, 0.6–1 mm. long, obtuse or rounded at apex; lateral bracteoles occasionally present and then shared by two contiguous flowers; anthers 1.2–2 mm. long and 0.6–0.9 mm. broad, obtuse at apex; Marquesas Islands. 2. *A. marquesensis*.

Inflorescences with flowers or fruits comparatively spaced on the rachis, with 5–8 branches 1.5–3.5 cm. long, the flowers or fruits often separated by 2–8 mm.

Leaf blades ovate to obovate, 5–14 × 2–8 cm., comparatively finely crenate-serrate, the teeth 3–7 per centimeter; flower-subtending bracts deltoid or broadly lanceolate, 0.5–1.5 mm. long; Solomon Islands and New Britain. 3. *A. maheshwarii*.

Leaf blades lanceolate, 4–9 × 1–3.5 cm., coarsely crenate-serrate, the teeth

2–5 per centimeter; flower-subtending bracts deltoid to lanceolate, 1–2 mm. long; New Caledonia. ..... 4. *A. solmsiana.*

Flowers subtended by a bract and two lateral bracteoles (or, when the ♀ flowers are paired and subtended by a single bract, then each with three bracteoles); ♂ flowers with a single stamen (and sometimes with a rudimentary adaxial pistil); endocarp (as far as known) verrucose or papillate.

Inflorescence branches or individual spikes (2–)3–11 cm. long at maturity, each with 25–100 flowers.

Pistillate flowers single (only very rarely, in one specimen of species no. 6, known to be sometimes paired); leaf blades attenuate at base and long-decurrent on petiole.

Petioles 1–10 mm. long, the leaf blades broadly elliptic or elliptic-obovate, usually 3.5–10 × 2–8 cm., averaging about twice as long as broad, obtuse to rounded at apex, sometimes slightly emarginate, rarely subacute, with (2–)3–5 crenations per centimeter; Society Islands. ..... 5. *A. polystachya.*

Petioles (4–)5–27 mm. long, the leaf blades lanceolate or narrowly elliptic, usually 6–14.5 × 1.5–4.5 cm., (2.5–)3–4 times as long as broad, bluntly acuminate at apex, with (2–)3–8 crenations per centimeter; Solomon Islands to Cook Islands. ..... 6. *A. diffusa.*

Pistillate flowers in pairs, each pair subtended by a single bract and each flower by three subequal bracteoles; petioles (10–)12–30 mm. long, the leaf blades elliptic, usually 5–12 × 2.5–5 cm., 2–2.5 times as long as broad, acute at base, obtusely cuspidate or acuminate at apex, with 2 (or 3) conspicuous crenations per centimeter; New Hebrides and Fiji. ..... 7. *A. swamyana.*

Inflorescence branches or individual spikes 1.2–3 cm. long at maturity, each with 10–50 flowers.

Flower-subtending bracts deltoid to ovate, attached to rachis at basal margin only, free on lateral margins; inflorescences with 4 or more lateral branches, not spicate; flowers comparatively spaced, sometimes disclosing 1–3 mm. of the rachis.

Leaf blades elliptic, usually 2.5–6 × 1.5–3.5 cm., averaging about twice as long as broad, callose-acute at apex, coarsely serrate with 2–4 conspicuous antrorsely projecting teeth per centimeter; inflorescences mostly terminal, with 4–8 lateral branches; New Zealand. ..... 8. *A. lucida.*

Leaf blades lanceolate, usually 5–11.5 × 1–3 cm., 3–5 times as long as broad, short-acuminate at apex.

Margins of leaf blades coarsely serrate; inflorescences mostly terminal; Kermadec Islands. ..... 9. *A. lanceolata.*

Margins of leaf blades crenate-serrate with 3–6 teeth per centimeter; inflorescences mostly axillary, with 4 or 5 lateral branches; New Caledonia. ..... 10. *A. rubricaulis.*

Flower-subtending bracts semipoculiform at anthesis; inflorescences axillary and terminal (if axillary, spicate in ultimate leaf axils; if terminal, 3-branched from base, the central branch 2-parted at apex of a short peduncle); flowers congested, essentially contiguous, rarely separated on the rachis by more than 1 mm.; leaf blades lanceolate to oblanceolate, 4–7 × 1–2 cm., 3–4 times as long as broad, obtuse at apex, inconspicuously crenate with 3–5 crenations per centimeter, the petioles 2–4 mm. long; Society Islands. ..... 11. *A. subfalcata.*

1. **Ascarina philippinensis** C. B. Robinson in Philipp. Jour. Sci. Bot. 4: 70. 1909; Swamy in Proc. Nat. Inst. Sci. India 19: 375. *fig. 2.* 1953.

Ascarina reticulata Merr. in Philipp. Jour. Sci. Bot. **12:** 263. 1917.

TYPIFICATION AND NOMENCLATURE. The holotype of *A. philippinensis*, *R. S. Williams 2541*, collected on Mt. Apo, Mindanao, Philippines, on March 31, 1905, was probably destroyed in the Bureau of Science herbarium at Manila; however, isotypes are available at K and NY. *Ascarina reticulata* is typified by *Ramos & Edaño* (Philipp. Bur. Sci.) *26399*, from Mt. Umingan, Luzon, Philippines; the holotype has presumably also been destroyed at Manila, but isotypes are deposited at A, K, and US.

DISTRIBUTION. Philippines, Borneo, and New Guinea, at elevations of 400 to 2,800 m.

Swamy has indicated that the putative differences between the two species described from the Philippines, such as leaf texture and color and the number of secondary nerves, are of little consequence. Having examined most specimens cited by him and many additional ones, I am inclined to agree that the available material from the Philippines and Borneo, as well as much of that from New Guinea, represents a single species. However, the variation in New Guinea is such that a detailed study should eventually be made to determine whether more than one New Guinean species in the group of *Ascarina* with two stamens should be recognized.

2. **Ascarina marquesensis** A. C. Smith, sp. nov. FIGURES 1–4.

Arbor dioecia ad 1.5 m. alta, trunco ad 8 cm. diametro, ramulis subteretibus apicem versus 2–4 mm. diametro ad nodos incrassatis, petiolorum basibus in vaginam 3–4 mm. longam connatis, stipulis veris minutis lanceolatis; petiolis gracilibus 5–20 mm. longis praeter basim anguste alatis, foliorum laminis subcoriaceis lanceolatis vel anguste ellipticis, 3.5–9 cm. longis, 1–4 cm. latis, basi attenuatis et in petiolum longe decurrentibus, apice subacutis vel obtusis saepe recurvato-calloso-emarginatis, margine praeter basim versus conspicue calloso-serratis, dentibus plerumque 4 vel 5 per centimetrum, costa supra subtiliter sulcata subtus prominenti, nervis secundariis subpatentibus utrinsecus 8–12 ut rete venularum utrinque prominulis; inflorescentiis ♂ solum visis terminalibus et nodos distales axillaribus, ubi axillaribus spicatis, ubi terminalibus compositis 3–5-ramosis, ramulis lateralibus spicatis et ad basim liberis, ramulo centrali interdum ramulos 1 vel 2 breves gerenti, spicis vel ramulis breviter pedunculatis 5–15 mm. longis et 15–20-floris, floribus congestis admodum contiguis; bractea sub flore late deltoidea, 0.6–1 mm. longa, 0.8–1.5 mm. lata, copiose glandulosa, apice obtusa vel rotundata, margine plerumque integra interdum suberosa; bracteolis lateralibus inter flores contiguos interdum praesentibus anguste ovatis vel lanceolatis ad 1.5 × 0.5 mm. sed plerumque minoribus;

FIGURES 1, 2. **Ascarina marquesensis** (from *Quayle 1319*): 1, tip of branchlet with ♂ inflorescences, × 2; 2, flowers on a portion of a ♂ spike, × 30.

staminibus 2 (raro 3, tertio tum parviore et adaxiali), antheris oblongis, 1.2–2 mm. longis, 0.6–0.9 mm. latis, basi et apice obtusis.

TYPIFICATION AND NOMENCLATURE. The type of the new species is *E. H. Quayle 1319*, from the Marquesas Islands. In citing this collection as *A. lanceolata* (*A. diffusa* in the present treatment), Swamy failed to note that its ♂ flowers have two (and rarely even three) stamens, a fact which excludes it from his "Group II." *Quayle 1319* further differs from *A. diffusa* in its short, congested, and few-flowered inflorescences.

DISTRIBUTION. Apparently endemic to the Marquesas and known to me only from the type collection. *A. marquesensis* is evidently a rare species. Quayle noted that he saw it only twice on the same ridge on the island of Nuku Hiva. Fosberg and Sachet (in Micronesica **8**: 43. 1972) mention a second Marquesan collection, *Sachet & Decker 1181*, from Hiva Oa, as representing *A. polystachya*. I have not seen this collection, which is not currently in the herbaria at BISH and US as indicated, but it may well represent the new species.

Marquesas Islands. NUKU HIVA: Hakaui upper plains, alt. 945–1,005 m., in moist, shady places on the side slope of a *Freycinetia*-covered ridge, Oct. 10, 1922 (bark smooth, burnt sienna in color; wood white, brittle), *Quayle 1319* (BISH, holotype; isotype also at BISH).

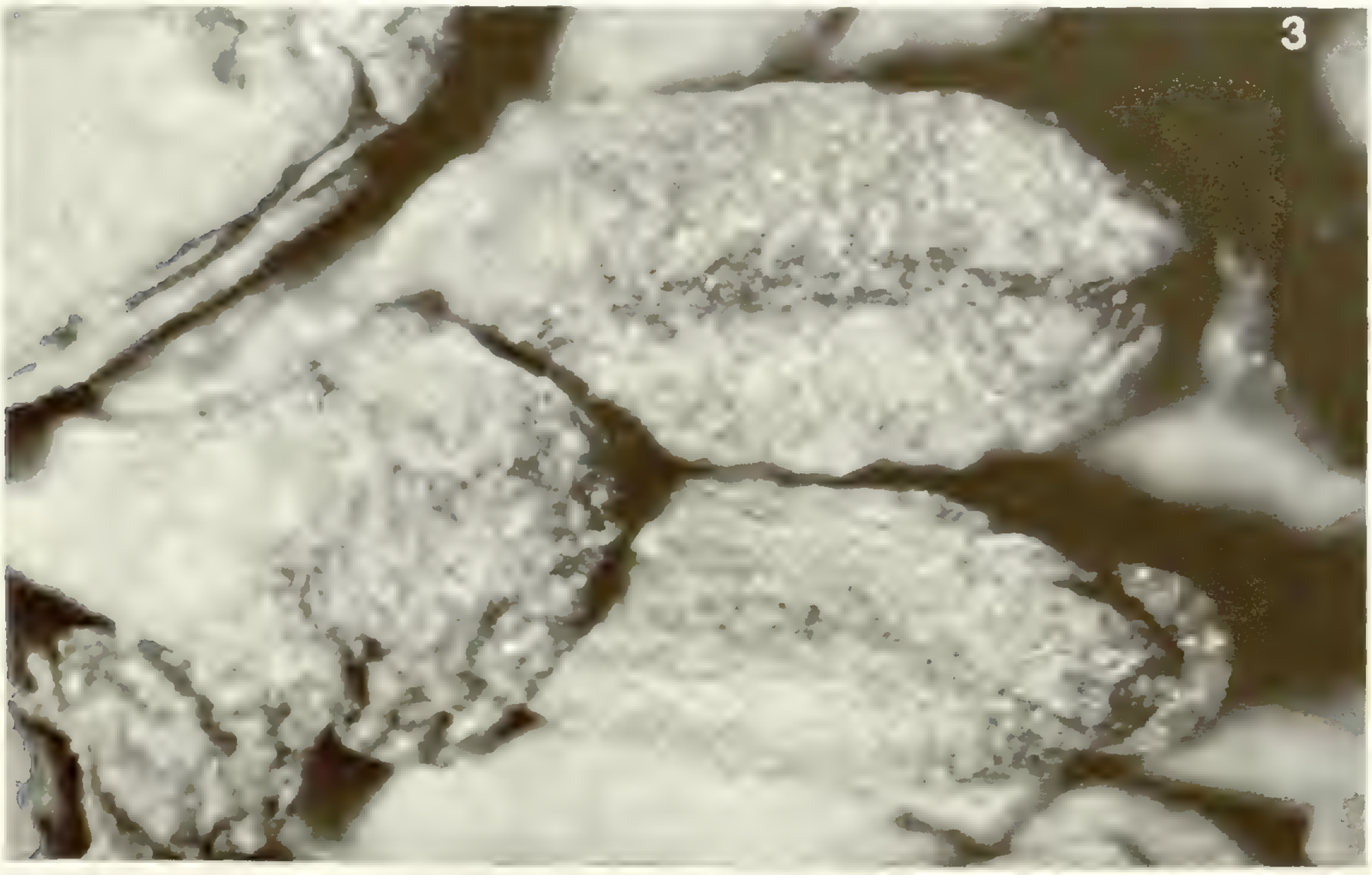
As a member of Swamy's "Group I," *A. marquesensis* seems related only to *A. philippinensis*, from which it differs in its proportionately narrower leaf blades, its comparatively few-branched inflorescences, and its anthers, which are smaller and obtuse at apex rather than subacuminate and with an obvious projecting connective. F. B. H. Brown (in Bishop Mus. Bull. **130**: 99. 1935) cited *Quayle 1319* as representing his *Weinmannia marquesana* var. *glabrata* (in which it has no type status), but Martin L. Grant removed the specimen from the Cunoniaceae at BISH and suggested that it might represent a new species of *Ascarina*.

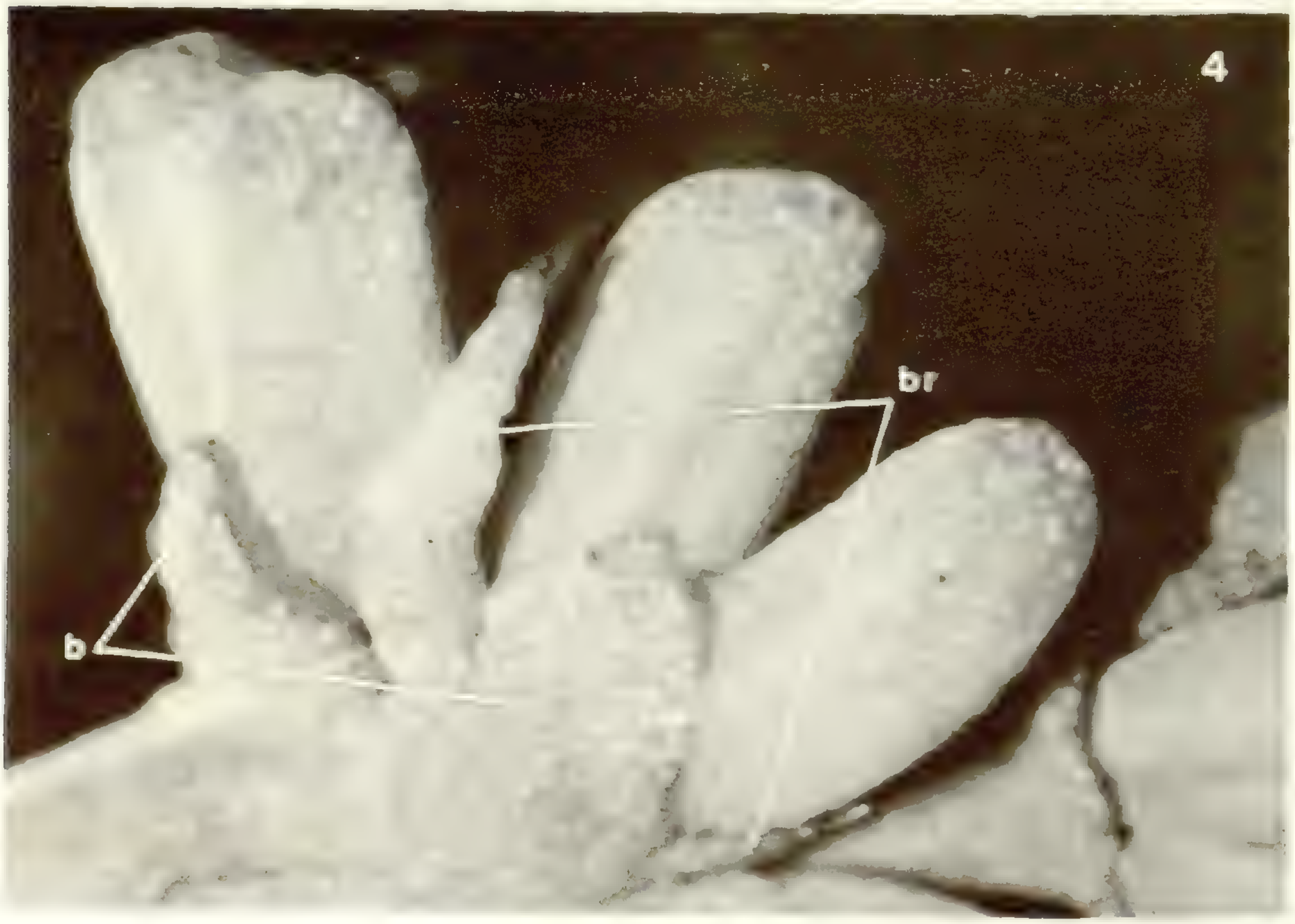
3. **Ascarina maheshwarii** Swamy in Proc. Nat. Inst. Sci. India 19: 377. *fig. 3*. 1953.

TYPIFICATION AND NOMENCLATURE. In describing this very distinct species, Swamy indicated *Kajewski 1681* (A) as the type of the ♀ plant and *Kajewski 2014* (A) as the type of the ♂ plant; both are from Bougainville. Since this procedure is not nomenclaturally permissible, and since the ♂ characters are perhaps more important in defining infrageneric relationships, I herewith designate *Kajewski 2014* (A) as the lectotype; isolectotypes are available at BISH, BM, and US. These specimens and several others were annotated by Swamy with an unpublished epithet.

DISTRIBUTION. New Britain and the Solomon Islands, at elevations of 600 to 2,075 m. Specimens from other Solomon Islands than Bougainville and San Cristobal, cited by Swamy, are now available and are here cited.

Solomon Islands. KOLOMBANGARA: *R. S. S. (Corner) 1195* (A, K), *1208* (A, K). GUADALCANAL: Monitor Creek, below Mt. Gallego, *R. S. S. (Whitmore) 6035* (A, K); Popomanasiu, *R. S. S. (Corner) 133* (A, K).





FIGURES 3, 4. **Ascarina marquesensis** (from *Quayle 1319*): 3, ♂ flower, showing two stamens subtended by a single bract, × 50; 4, contiguous ♂ flowers, showing subtending bract and occasional lateral bracteoles, × 30 (b = flower-subtending bract; br = lateral bracteole).

4. **Ascarina solmsiana** Schlechter in Bot. Jahrb. **39**: 94. 1906; Swamy in Proc. Nat. Inst. Sci. India **19**: 377. *fig. 4.* 1953.

TYPIFICATION. The holotype, *Schlechter 15679*, collected in January, 1903, in New Caledonia, was probably destroyed at B, but isotypes are available at BM and K.

DISTRIBUTION. New Caledonia; Swamy cites only the type collection.

5. **Ascarina polystachya** J. R. & G. Forster, Char. Gen. Pl. 59. *t. 59.* 1775, ed. 2. 118. *t. 59.* 1776; Seem. Fl. Vit. 258. 1868; Drake, Ill. Fl. Ins. Mar. Pac. 277. 1892; Swamy in Proc. Nat. Inst. Sci. India **19**: 379. *fig. 7.* 1953.

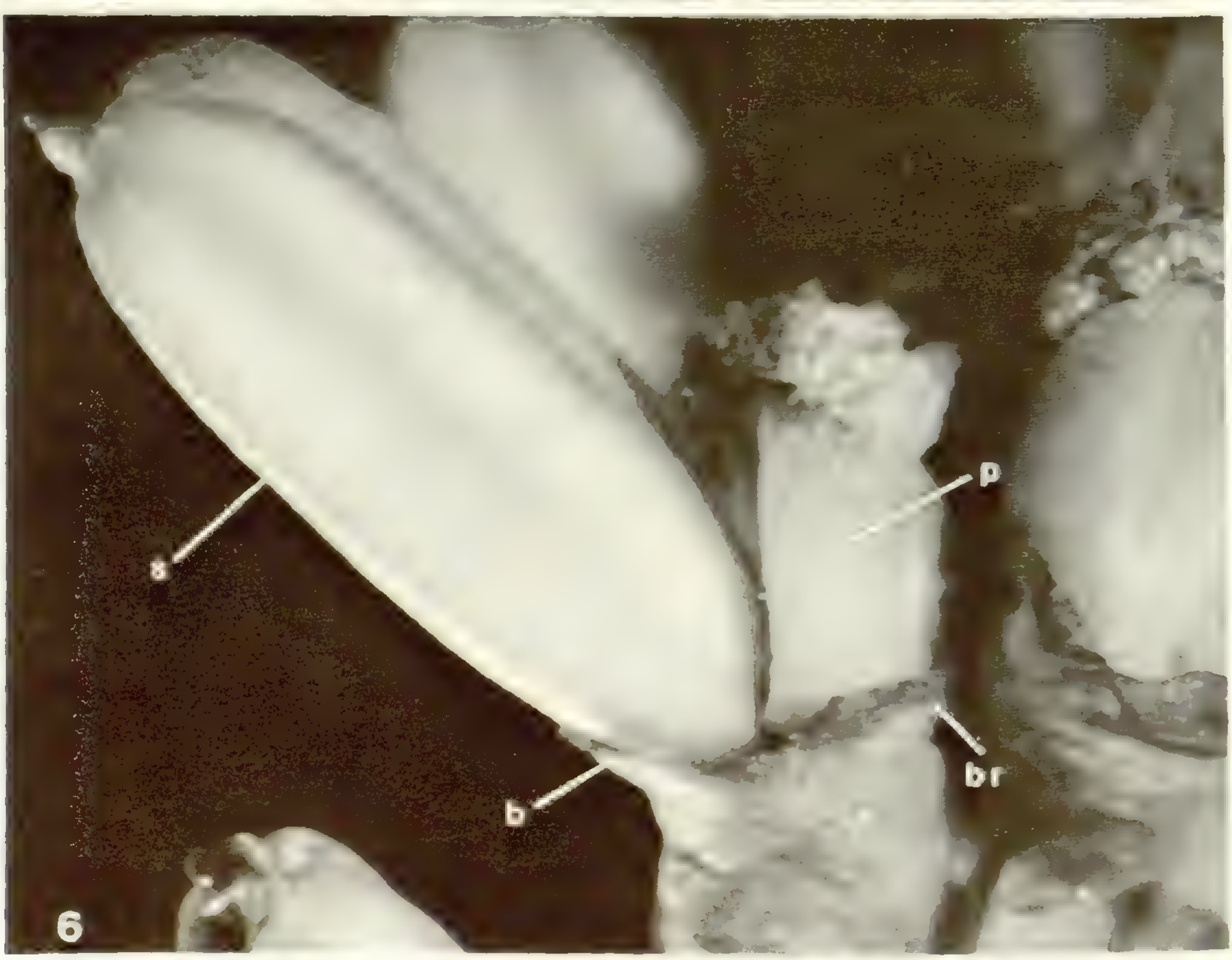
Ascarina raiateensis J. W. Moore in Occas. Pap. Bishop Mus. **10**(19): 7. 1934.

TYPIFICATION AND NOMENCLATURE. In proposing the genus and species the Forsters did not cite a specimen. Their illustration shows both ♂ and ♀ inflorescences and therefore would seem to have been based on at least two specimens. One of these, probably the ♀ specimen, was their own, which was listed by both Seemann and Drake. The ♂ specimen was presumably a Banks and Solander collection from the first Cook voyage. This is the specimen described by Solander in his manuscript Prim. Fl. Ins. Oc. Pac. 338 as *Psilotum serratum*, a binomial listed in synonymy by both Seemann and Drake. An illustration (*t. 112*) also exists among Parkinson's unpublished drawings. Since the Forsters in 1775 had access to the Banks and Solander collection, Solander's description, and Parkinson's drawing, and since the ♂ plant is perhaps more significant than the ♀, I herewith designate as lectotype of *A. polystachya* the BM specimen of *Banks & Solander*, collected in 1769 in Tahiti; an isolectotype is available at BISH.

The holotype of *A. raiateensis* is *Moore 178* (BISH), from Temehani Plain, Raiatea. I believe that Swamy's reduction of this to *A. polystachya* is correct. Moore indicates that his taxon differs from *A. polystachya* in its smaller, short-petiolate leaves, shorter inflorescences, and crowded fruits with more distinctly lobed stigmas. However, among the available Tahitian specimens are several that seem to agree precisely with Moore's type: *Grant 3764, 4235*, *MacDaniels 1344*, and *U. S. Expl. Exped.* (GH, p. p., US 40535, p. p.; the material obviously came from more than one plant). Small, short-petiolate leaves do not seem particularly correlated with altitude.

DISTRIBUTION. Endemic to the Society Islands and thus far known only from Tahiti and Raiatea, at elevations of 400 to 1,650 m. A few additional specimens not listed by Swamy are here cited.

Society Islands. TAHITI: Mt. Aorai and vicinity, *Fosberg & Sachet 54704* (GH, NY, US), *Gillett 2241* (BISH), *Grant 3764* (A, BISH), *Webster 15272* (BISH,



FIGURES 5, 6. **Ascarina diffusa** (5 from *Christophersen 571*, 6 from *Bernardi 12913*): 5, tip of branchlet with ♀ inflorescences, × ½; 6, ♂ flower, showing subtending bract, a lateral bracteole, the solitary stamen, and a sterile pistil, × 30 (b = flower-subtending bract; br = lateral bracteole; s = stamen; p = pistil).

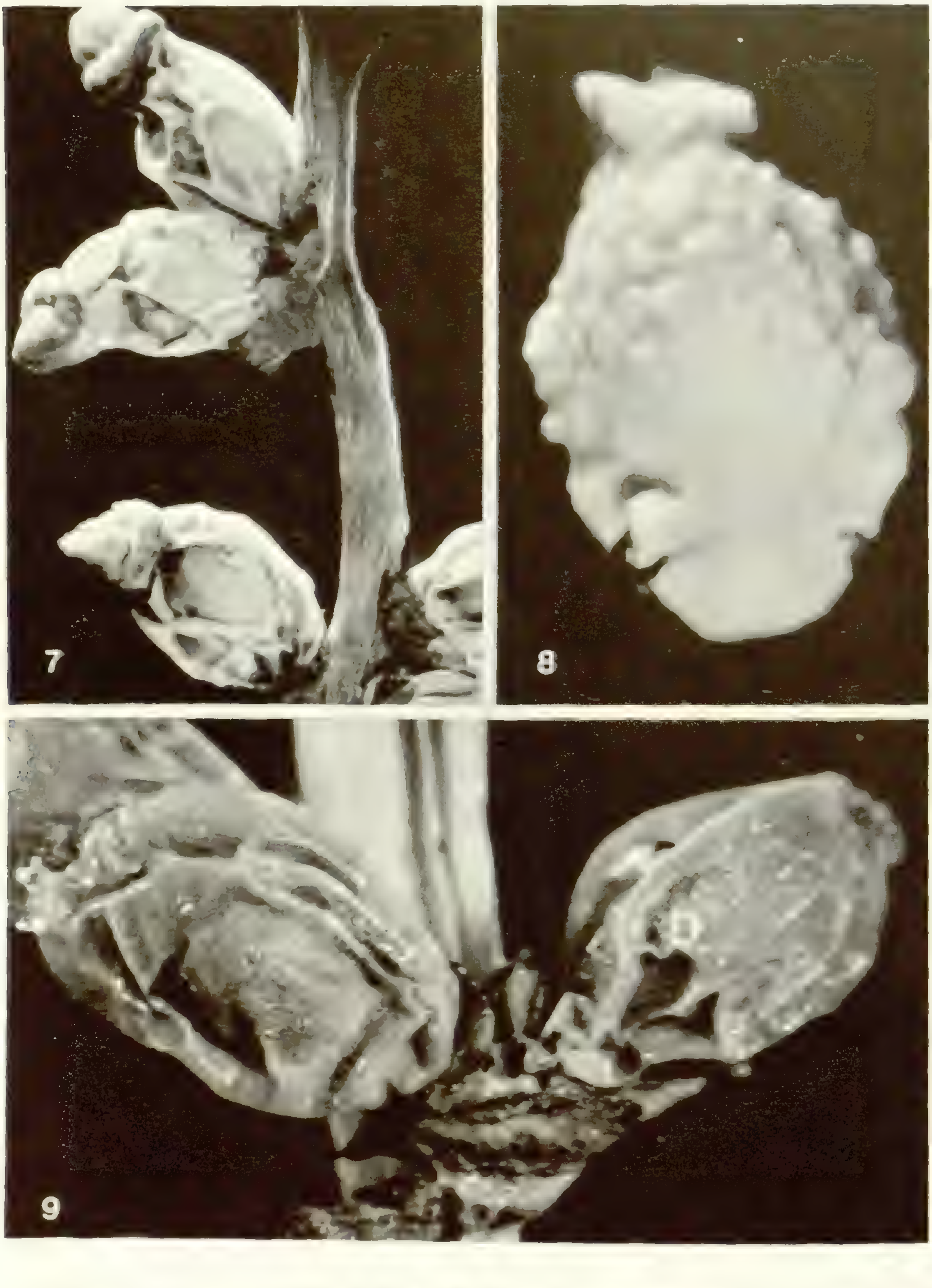
DAV); Mt. Orofena, *Grant 4235* (BISH); Lake Vaheria, *MacDaniels 1272* (BISH), *1615* (BISH); Mt. Roniu, *Grant 3918* (BISH).

6. Ascarina diffusa A. C. Smith, sp. nov. FIGURES 5–10.

Ascarina lanceolata sensu Drake, Ill. Fl. Ins. Mar. Pac. 277, quoad spec. Ins. Sam. 1892; Swamy in Proc. Nat. Inst. Sci. India **19:** 377, excl. spec. Ins. Soc. et Marq. *fig. 5.* 1953; J. W. Parham, Pl. Fiji Isl. ed. *2.* 311, quoad var. *lanceolata.* 1972; non Hooker f.

Arbor dioecia vel raro monoecia 4–12(–25) m. alta, ramulis subteretibus apicem versus 1.5–2.5 mm. diametro ad nodos incrassatis, petiolorum basibus in vaginam 1–3 mm. longam connatis, stipulis veris lanceolatis 2–3 mm. longis; petiolis gracilibus (4–)5–27 mm. longis praeter basim anguste alatis, foliorum laminis subcoriaceis lanceolatis vel anguste ellipticis, (4.5–)6–14.5 cm. longis, (1–)1.5–4.5 cm. latis, plerumque 3–4-plo longioribus quam latioribus, basi attenuatis et in petiolum longe decurrentibus, apice obtuse acuminatis (apice ipso ultra dentem ultimum vulgo 5–15 mm. longo), margine praeter basim versus calloso-crenato-serratis, dentibus (2–)3–8 per centimetrum, costa supra subtiliter sulcata subtus prominenti, nervis secundariis patentibus vel adscendentibus utrinsecus 15–25 utrinque prominulis vel supra subplanis, rete venularum irregulariter anastomosanti utrinque prominulo vel subtiliter impresso; inflorescentiis terminalibus et nodos 1–3 distales axillaribus, ubi axillaribus spicatis, ubi terminalibus compositis 4- vel 5-ramosis et saepe bracteis lanceolatis subfoliaceis ad 6 mm. longis subtentis, ramulis lateralibus spicatis et ad basim plerumque liberis, ramulis 2 vel 3 centralibus pedunculo communi enatis, pedunculis primariis et secundariis 8–30 mm. longis, spicis vel ramulis (2–)3–11 cm. longis plerumque 50–100-floris (floribus ♀ inflorescentiae ramulis raro tantum 10), floribus laxe dispositis, rhachidis partibus nudis plerumque 2–6 mm. longis; bractea sub flore deltoidea, 0.5–1 mm. longa, 0.5–1.2 mm. lata, obscure glandulosa, apice subacuta vel rotundata, bracteolis lateralibus 2 similibus sed parvioribus 0.2–0.9 mm. longis latisque; stamine in floribus ♂ solitario, pistillo adaxiali sterili oblongo ad 1 × 0.5 mm. cum stigmate bilobato conspicuo interdum praesenti, anthera oblonga, 2–3 mm. longa, 0.8–1.2 mm. lata, basi obtusa, apice 0.2–0.3 mm. longo conspicue mucronata; floribus ♀ ut ♂ bractea unica et bracteolis 2 subtentis, floribus ♀ contiguis rarissime bractea unica subtentis et tum utroque 3-bracteolato; pistillo ellipsoideo vel ovoideo post anthesin et fructu 2–3 mm. longo et 1.5–2 mm. lato, stigmate conspicuo 0.8–1.3 mm. lato, fructus endocarpio distaliter conspicue papillato basi rotundato vel obtuso apice obtuse projecto.

TYPIFICATION AND NOMENCLATURE. The species here described as new was interpreted by Swamy as *A. lanceolata* Hooker f., but it must exclude the type collection of that species and also the material from the Society and Marquesas Islands cited by Swamy. As type of the new species I designate *Smith 7887*, a ♂ Fijian collection with many duplicates, cited below.



FIGURES 7–9. **Ascarina diffusa** (7 and 8 from *Christophersen 571*, 9 from *Parks 22521*): 7, portion of ♀ spike, × 10; 8, endocarp, × 30; 9, rare instance of paired ♀ flowers subtended by a single bract, × 20.

DISTRIBUTION. Uncommon in mountainous areas from the Solomon Islands (Bougainville) to the Cook Islands (Rarotonga), reported from forests or open crests at elevations of 350 to 1,825 m. (to 1,825 m. on Bougainville, 900 m. on Tanna, 500 m. on Ngau, 1,600 m. on Savaii, 680 m. on Upolu, and nearly 1,000 m. on Rarotonga).

FIGURE 10. **Ascarina diffusa** (from *Smith 7887*): lower surface of apical portion of leaf blade. × 10. FIGURES 11, 12. **Ascarina swamyana** (from *Smith 908*): 11, lower surface of apical portion of leaf blade. × 10; 12, tip of branchlet with ♀ inflorescences. × ½.

LOCAL NAMES. Recorded local names are *langolango* (Fiji), *togo vau* or *fiti* (Samoa), and *kaiatea* (Rarotonga).

Solomon Islands. BOUGAINVILLE: Lake Luralu, Koniguru, Buin, *Kajewski 2173* (A, BISH); Lake Loloru and rim of crater, *Schodde & Craven 3915* (A, K, US), *NGF (Lavarack & Ridsdale) 31407* (A, K). **New Hebrides.** TANNA: mountains in vicinity of Lamwinaoura, *Bernardi 12913* (G, US); in montane forests, *Bernardi 13132* (A, G, US). ANEITYUM: above Anelgauhat Bay, *Kajewski 863* (A, BISH, K, NY, US). **Fiji.** VITI LEVU: without further locality, *Graeffe* (K). NGAU: northern spur of Mt. Ndelaitho, toward Navukailangi, June 22, 1953, *Smith 7887* (US 2190693, holotype; isotypes at BISH, GH, K, L, NY, P, S, SUVA, UC). FIJI, without further locality, *U. S. Expl. Exped.* (GH, K, US 40438). **Samoa.** SAVAII: Mt. Maugaloa, *Vaupel 494* (BISH, K, NY, US); above Matavanu, *Christophersen & Hume 1996* (BISH, US), *2014* (A, BISH, US), *2153* (BISH, US), *2167* (K, NY); Tuisivi Range, *Christophersen 820* (BISH, K, NY). UPOLU: Mt. Fao, *Christophersen 571* (A, BISH). SAMOA, without further locality, *Whitmee* (GH), *93* (K), *Powell 237* (K). **Cook Islands.** RAROTONGA: Mt. Ikurangi, *Wilder 827* (BISH), *Philipson 10257* (US); Mt. Manngotia, *H. E. & S. T. Parks 22248* (K, UC, US), *22521* (BISH, GH, K, NY, UC, US); in mountains, *Cheeseman 645* (K).

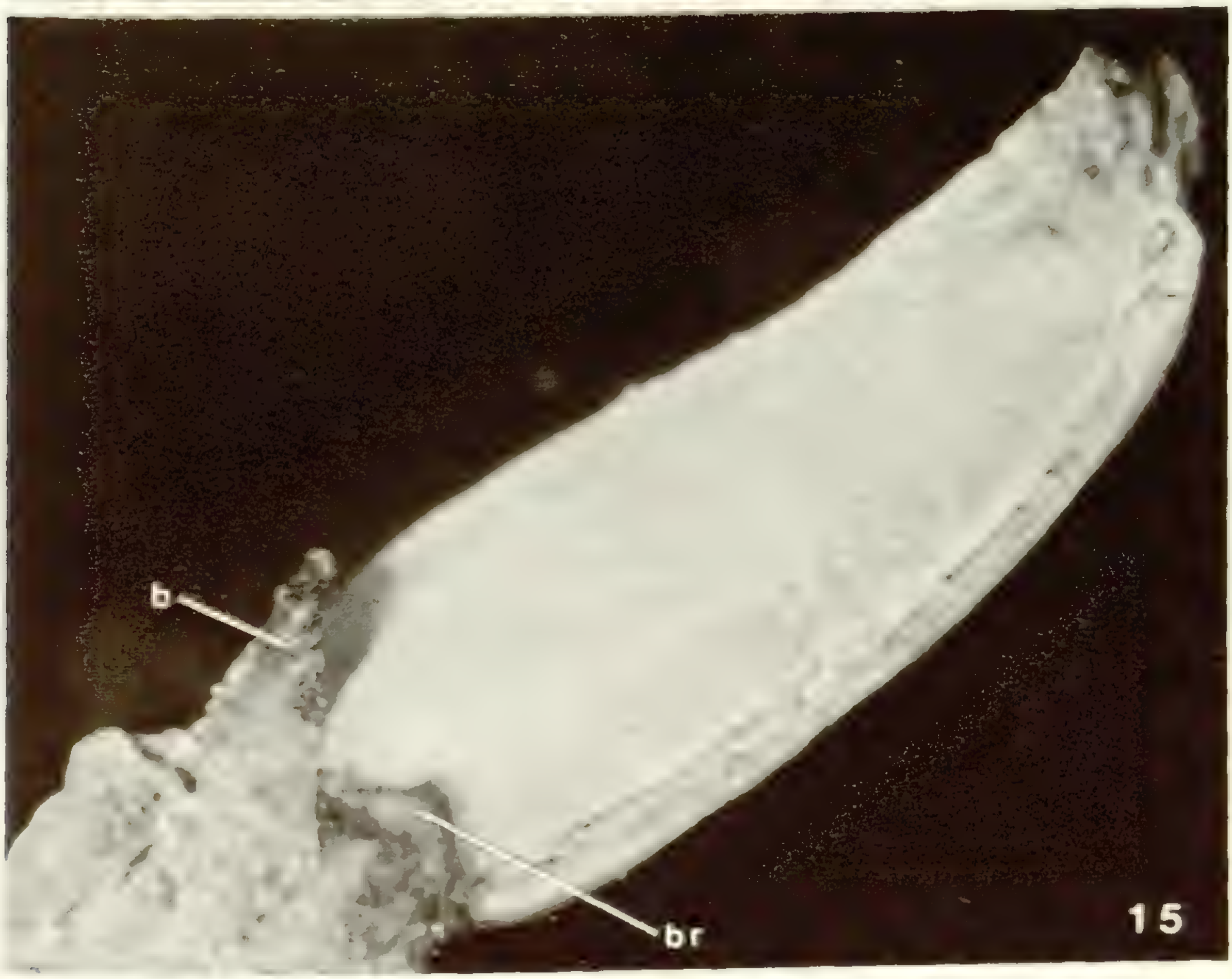
As noted by Swamy, the ♂ flower of this species occasionally bears an incipiently developed, adaxially placed pistil; such flowers have been seen on specimens from the New Hebrides (*Bernardi 12913*) and Fiji (*U. S. Expl. Exped., Smith 7887*). It must also be noted that the primary character separating this species from the next (*A. swamyana*), relative to the single or paired ♀ flowers, is not absolute. On a single collection of *A. diffusa* from Rarotonga (*Parks 22521*) gradations have been noted in this character from the usual ♀ flower to contiguously appressed ♀ flowers (each still subtended by its own bract) to a rare situation in which two contiguous ♀ flowers are subtended by a single bract (FIGURE 9).

7. **Ascarina swamyana** A. C. Smith, sp. nov. FIGURES 11–17.

Ascarina lanceolata sensu Seem. in Bonplandia **9:** 259. 1861, Viti, 442. 1862, Fl. Vit. 258, p. p. *t. 74*, solum quoad *fig. 4*. 1868; Drake, Ill. Fl. Ins. Mar. Pac. 277, quoad spec. Ins. Vit. 1892; J. W. Parham, Pl. Fiji Isl. 223. 1964; non Hooker f.

Ascarina lanceolata var. *smithii* Swamy in Proc. Nat. Inst. Sci. India **19:** 378. *fig. 6*. 1953; J. W. Parham, Pl. Fiji Isl. ed. 2. 311. 1972.

Arbor gracilis dioecia vel raro monoecia 5–10 m. alta, ramulis subteretibus apicem versus 1.5–3 mm. diametro ad nodos incrassatis, petiolorum basibus in vaginam 2–3 mm. longam connatis, stipulis veris minutis lanceolatis; petiolis gracilibus (10–)12–30 mm. longis canaliculatis apicem versus anguste alatis, foliorum laminis subcoriaceis ellipticis, (4–)5–12 cm. longis, (2–)2.5–5 cm. latis, 2–2.5-plo longioribus quam latioribus, basi acutis et in petiolum breviter decurrentibus, apice obtuse callosis et cuspidatis vel acuminatis (apice ipso ultra dentem ultimum 3–15 mm. longo), margine praeter basim versus calloso-crenato-serratis, dentibus 2



FIGURES 13–15. **Ascarina swamyana** (from *Kajewski 152*): 13, portion of ♂ spike, × 10 (s = stamen); 14, portion of ♀ spike, × 10 (p = pistil); 15, ♂ flower, showing subtending bract, a lateral bracteole, and the solitary stamen, × 30 (b = flower-subtending bract; br = lateral bracteole).

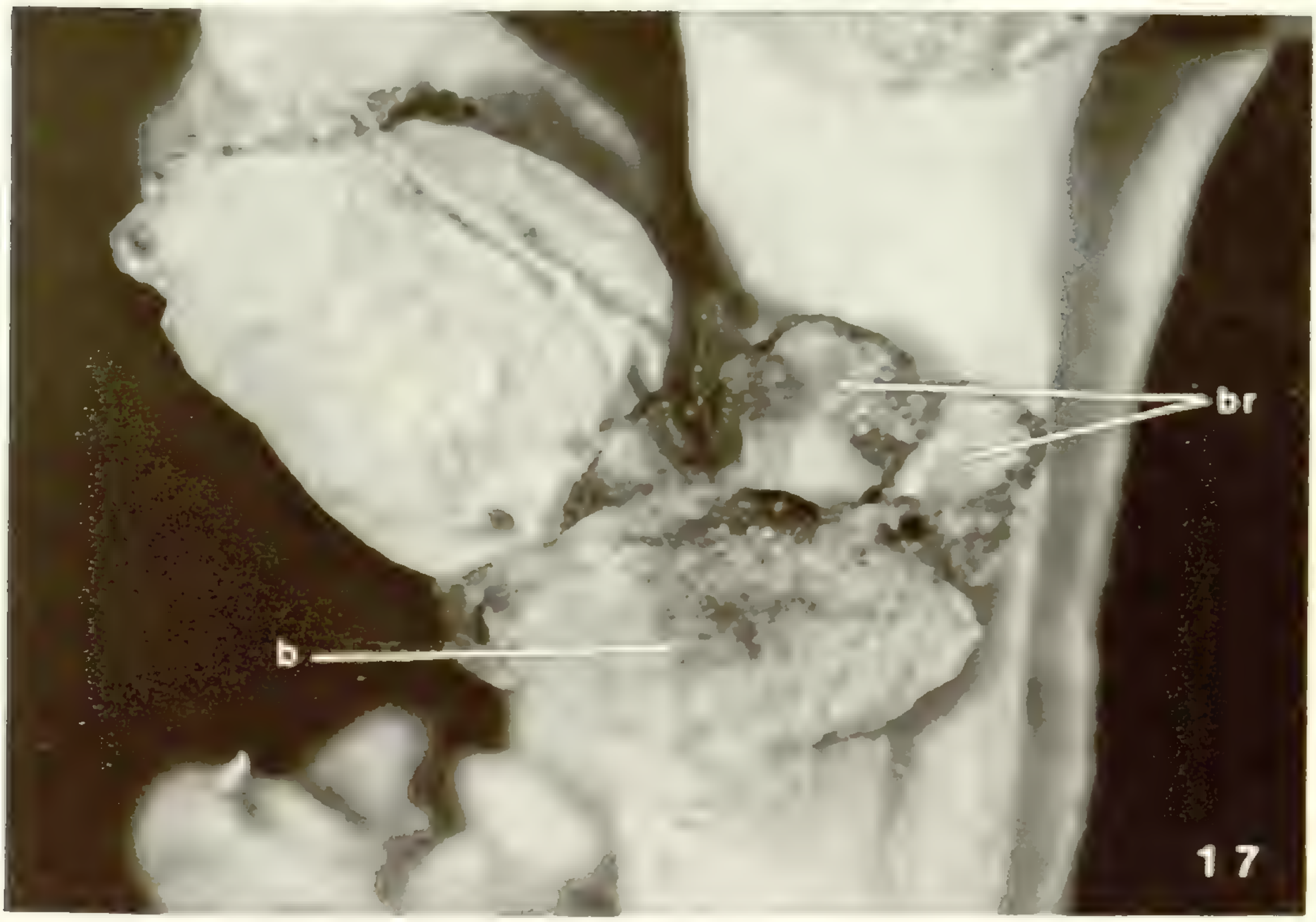
(interdum 3) per centimetrum, costa supra acute sulcata subtus prominenti, nervis secundariis patentibus utrinsecus 10–18 utrinque prominulis, rete venularum irregulariter anastomosanti utrinque prominulo vel plano; inflorescentiis terminalibus et nodos 1–3 distales axillaribus, ubi axillaribus spicatis, ubi terminalibus compositis 4- vel 5-ramosis, ramulis lateralibus spicatis et ad basim liberis, ramulis 2 vel 3 centralibus pedunculo communi enatis, pedunculis primariis et secundariis 5–20 mm. longis, spicis vel ramulis (2–)3–7 cm. longis plerumque 25–50-floris, floribus laxe dispositis, rhachidis partibus nudis plerumque 1–3 mm. longis; bractea sub flore ♂ deltoidea vel reniformi, 0.7–1 mm. longa, 0.8–1.5 mm. lata, copiose glandulosa, apice subacuta vel rotundata, bracteolis lateralibus 2 similibus sed parvioribus 0.3–0.5 × 0.5–0.8 mm.; stamine solitario, anthera oblonga, 2.5–3 mm. longa, 1–1.2 mm. lata, basi obtusa, apice 0.2–0.3 mm. longo obtuso mucronata; floribus ♀ binis bractea unica subtentis utroque 3-bracteolato, bracteis bracteolisque eis ♂ similibus; pistillo subgloboso vel ovoideo post anthesin et fructu 0.7–1.5 mm. longo et 0.7–1.2 mm. lato, stigmate conspicuo 0.8–1 mm. lato, fructus endocarpio verrucoso apice obtuso.

TYPIFICATION AND NOMENCLATURE. The taxon here described as a new species was first misidentified by Seemann, on the basis of his no. *564*, as *A. lanceolata* Hooker f., but later in *Flora Vitiensis* Seemann's concept also included material from New Caledonia, the Kermadec Islands, and Samoa. Concerning the figures in Seemann's 1868 illustration, only those showing two flowering branches seem to be original. Of these, *figure 4* (♀) is probably based on *Seemann 564* and so belongs with the present species. *Figure 1* (♂) is probably based on the Powell specimen listed by Seemann and is referable to *A. diffusa*. *Figures 2*, *3*, *5*, and *6* were copied from sketches made by Solms-Laubach and cannot be confidently identified. In assigning specific rank to Swamy's variety I utilize the same type specimen, but I prefer to replace his epithet with one that will commemorate his valuable work on the Chloranthaceae and many other primitive angiosperm families. The type of the new species is *Smith 908*, a Fijian collection with many duplicates, cited below.

DISTRIBUTION. Infrequent in the New Hebrides and Fiji, known only from montane forests and crest thickets at elevations of 760 to 1,241 m.

New Hebrides. AMBRYM: Mt. Toüo, *Aubert de la Rüe* (A, P). TANNA: Mt. Tokosh Meru, *Kajewski 152* (A, K, NY). **Fiji.** VITI LEVU. NAMOSI: Mt. Voma, *Seemann 564* (GH, K), *Fiji Dept. Agr. 612* (SUVA). TAVEUNI: summit of Mt. Uluingalau, Jan. 3, 1934, *Smith 908* (GH, holotype and also holotype of *A. lanceolata* var. *smithii*; isotypes at BISH, BO, K, NY, P, S, UC, US, Y).

Although Swamy considered this taxon and the preceding only varietally distinct, the differentiating characters appear to me worthy of specific recognition. The uniform occurrence of paired ♀ flowers in the present taxon was noted by Swamy, but this situation may very rarely also occur in *A. diffusa*, as noted under that species. In other respects, *A. swamyana*



FIGURES 16, 17. **Ascarina swamyana** (from *Smith 908*): 16, paired ♀ flowers subtended by a single bract. × 30; 17, same with one pistil removed to show two of the flower-subtending bracteoles. × 30 (b = flower-subtending bract; br = bracteoles).

differs from *A. diffusa* in its often longer petioles, its proportionately broader and fewer-nerved leaf blades which are only short-decurrent on

the petiole and have more coarsely crenate-serrate margins, and its apparently smaller pistils and fruits.

8. **Ascarina lucida** Hooker f. Fl. Novae-Zel. 1: 228. 1853; Cheeseman, Man. New Zeal. Fl. 598. 1906, Ill. New Zeal. Fl. 2: *pl. 166*. 1914; Swamy in Proc. Nat. Inst. Sci. India 19: 379, p. p. excl. spec. Ins. Kermadec. *fig. 8*. 1953; Allan, Fl. New Zeal. 1: 172. 1961.

TYPIFICATION AND NOMENCLATURE. In his original publication of this binomial Hooker cited two collections, "Northern Island, Totara-nui, *Banks and Solander*," and "Swamps, Wairarapa Valley, *Colenso*," and he also listed "*Trophis lucida Banks et Sol.* MSS. et Ic." Cheeseman in 1914 indicated that Banks and Solander first obtained the species in January, 1770, in Queen Charlotte Sound (Marlborough Province, South Island). The Colenso locality is in Wellington Province, North Island. Although it would seem that the Banks and Solander material is a logical choice as the lectotype, a botanist familiar with New Zealand plants should make such a decision after examining all the material that may have been seen by Hooker. The three Kermadec Island specimens cited by Swamy should be excluded from the species, at least in my present opinion.

Cheeseman's 1914 illustration shows that sometimes a rudimentary pistil occurs adaxially in ♂ flowers, as noted above for *A. diffusa* (FIGURE 6).

9. **Ascarina lanceolata** Hooker f. in Jour. Linn. Soc. Bot. 1: 127, 129 as *Asimina l.*, sphalm. 1856; Cheeseman, Man. New Zeal. Fl. 597. 1906.

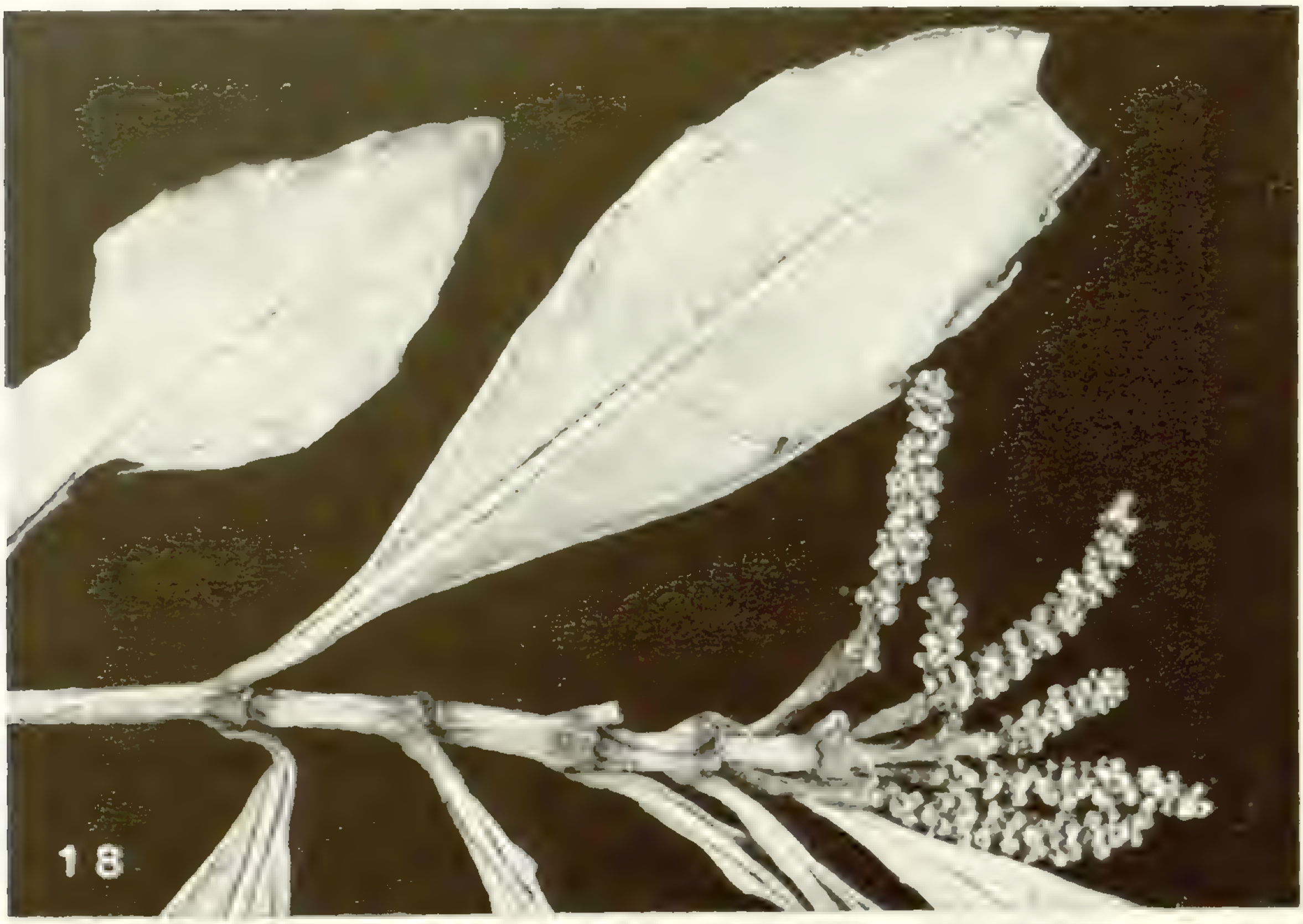
Ascarina lucida sensu Swamy in Proc. Nat. Inst. Sci. India 19: 379, p. p. 1953; non sensu typi.

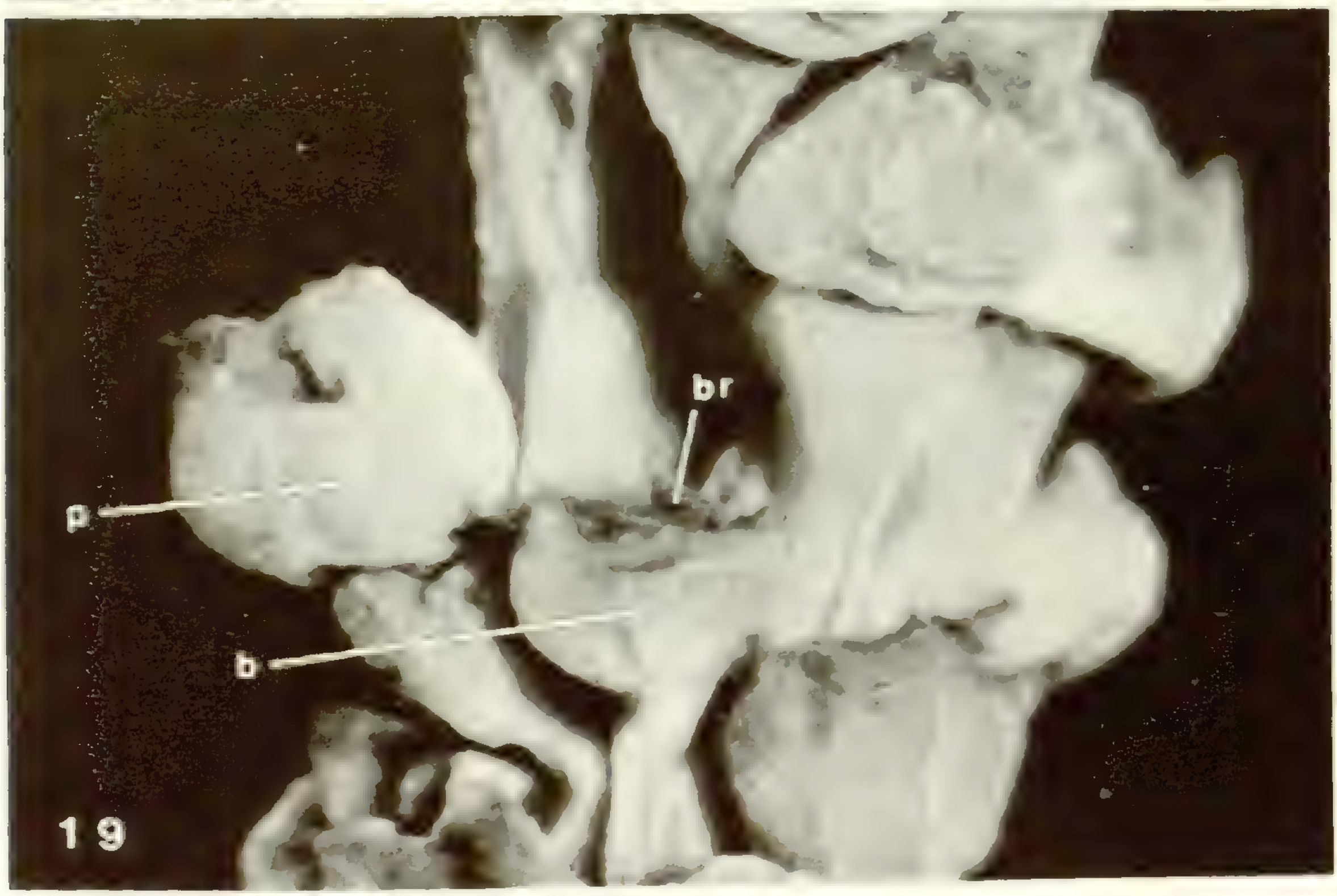
Ascarina lucida var. *lanceolata* Allan, Fl. New Zeal. 1: 173. 1961.

TYPIFICATION AND NOMENCLATURE. *Ascarina lanceolata* is typified by a *MacGillivray* (K) specimen (H. M. S. *Herald* Bot. *982*) collected July 24, 1854, on Raoul Island ("Sunday Island"), Kermadec Islands.

DISTRIBUTION. Kermadec Islands.

The MacGillivray specimen was cited by Swamy, without indication of its type status, as representing *A. lucida* Hooker f. In thus considering *A. lucida* as occurring in both New Zealand and the Kermadec Islands Swamy was anticipated by Hooker himself (Handb. New Zeal. Fl. 253. 1864), who in discussing *A. lucida* commented, "I find that the Kermadec Island plant with larger leaves, which I distinguished as *A. lanceolata* (Journ. Linn. Soc. i. 129) is only a variety of the New Zealand one." Certainly many recent students of the New Zealand flora concur in this opinion, although the trinomial seems to have been proposed only by Allan in 1961. In view of the paucity of good differentiating characters in *Ascarina* and our still very incomplete knowledge of the genus, I be-





FIGURES 18, 19. **Ascarina subfalcata** (from *Moore 657*): 18. tip of branchlet with ♀ inflorescences, × 2; 19. portion of ♀ spike with one pistil removed, showing flower-subtending bract and lateral bracteoles, × 30 (b = flower-subtending bract; br = lateral bracteole; p = pistil).

lieve that *A. lanceolata* is best considered a Kermadec Island endemic at the specific level for the time being. In foliage it is very readily distinguishable from *A. lucida*, as indicated by Cheeseman in 1906. Dr. W.

R. Sykes (in litt.) indicates that the seeds of the Kermadec Island *Ascarina*, like those of *A. lucida*, are white or sometimes have a pale reddish flush, whereas those of the Rarotonga plant (herein referred to *A. diffusa*) are shining black or dark brown.

10. **Ascarina rubricaulis** Solms in DC. Prodr. **16**(1): 478. 1869; Swamy in Proc. Nat. Inst. Sci. India **19**: 380. *fig. 9*. 1953.

TYPIFICATION AND NOMENCLATURE. Solms originally cited three New Caledonian collections: *Pancher*, *Deplanche*, and *Vieillard 1212*. Pancher sheets of the species, without number or locality, are available at A, BM, and K. *Vieillard 1212* is duplicated at A, BM, GH, and K. Like certain other Vieillard collections, this number appears to combine material from two localities, Balade and Wagap. Although Swamy has indicated the Vieillard sheets available to him as "cotypes," I do not believe that he has thus adequately lectotypified the species; this task remains for a student of New Caledonian plants.

The binomial "*A. lurida*" seems to have originated inadvertently through Solms's listing of "*A. lurida* Hook. f., J. Linn. Soc. 1: 129, solum nomen." This name has no nomenclatural status and presumably refers to a herbarium misidentification of a New Caledonian plant as *A. lucida*.

11. **Ascarina subfalcata** J. W. Moore in Bishop Mus. Bull. 102: 26. 1933. FIGURES 18, 19.

TYPIFICATION AND NOMENCLATURE. The holotype is *Moore 657* (BISH), collected on the south end of Opoa Mountain, Raiatea, Society Islands, on March 5, 1927. I believe that this species is very distinct from Swamy's concept of *A. lanceolata*, the binomial to which he reduced it.

DISTRIBUTION. Known only from the type collection and presumably endemic to the island of Raiatea, where it is known at an altitude of 200 m.

Ascarina subfalcata has much shorter inflorescences and more congested flowers than *A. diffusa* (i.e. *A. lanceolata* sensu Swamy, non Hooker f.). It is also quite distinct from its congeners in having its flower-subtending bracts semipoculiform at anthesis rather than attached only by the base, and in its comparatively small, subglobose pistil. Its relationship is probably with *A. lanceolata* (sensu vero) rather than with *A. diffusa*. One may note that the three species now seemingly endemic to the Society and Marquesas Islands are not closely interrelated; *A. marquesensis* is probably derived from a forbear of *A. philippinensis*, *A. polystachya* from an ancestry suggestive of *A. diffusa*, and *A. subfalcata* from a plant resembling *A. lanceolata*.

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THE GENUS LINDENIA (RUBIACEAE)

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THE SMALL RUBIACEOUS genus *Lindenia* Bentham is probably better known to plant geographers than to other botanists. Its strikingly disjunct distribution was first noted by Seemann (1862), but no serious attempt to explain this phenomenon has been made. Indeed, the genus has never been reviewed on a worldwide basis, although as many as six species have been proposed by various authors since its establishment in 1841. As treated here, *Lindenia* consists of three species, of which one is endemic to Central America, one to Fiji, and one to New Caledonia. A new form of the American species (*L. rivalis* f. *glabra*) is described, and two other taxa, *L. acuminatissima* Wernh. and *L. radicans* Wernh., are excluded from the genus.

Appreciation is expressed to the administrators of the following institutions who have made their herbarium collections available: Arnold Arboretum of Harvard University (A); Amherst College Herbarium (deposited at University of Massachusetts) (AC); Bernice P. Bishop Museum (BISH); British Museum (Natural History) (BM); Field Museum of Natural History (F); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); Department of Botany, University of Massachusetts (MASS); Missouri Botanical Garden (MO); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P); Departments of Agriculture and Forestry, Suva, Fiji (SUVA); University of California, Berkeley (UC); and U. S. National Herbarium (US).

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Lindenia Bentham, Pl. Hartweg. 84. 1841, in Hooker's Icon. Pl. **5**: *t. 476*. 1842; Endlicher, Gen. Pl. Suppl. **2**: 53. 1842; Bentham, Pl. Hartweg. 351. 1857; Hooker in Bot. Mag. **87**: *t. 5258*. 1861; Seem. in Bonplandia **10**: 33. 1862, Fl. Vit. 128. 1866; Hooker f. in Bentham & Hooker f., Gen. Pl. **2**: 51. 1873; K. Schum. in Engler & Prantl, Nat. Pflanzenfam. IV. **4**: 37. 1891; Standley in N. Am. Fl. **32**: 92. 1921, in Field Mus. Nat. Hist. Bot. Ser. **18**: 1325. 1938; A. C. Smith in Jour. Arnold Arb. **36**: 288. 1955; Standley & Williams in Fieldiana **24**(11): 118. 1975.

Siphonia sensu Bentham, Pl. Hartweg. 84. 1841, non D. Rich. ex Schreber (1791).

Riverine shrubs with stipulate, petiolate leaves; leaf blades chartaceous and drying dark, often red-brown above, paler beneath, acute to

attenuate at base and decurrent on petiole, acute to somewhat acuminate and often asymmetric at apex, with entire, revolute margin, the costa conspicuous, plane to somewhat raised and canaliculate above, prominent and rounded beneath, the secondary nerves 5–10 per side, plane to prominulous above, sharply elevated beneath, the tertiary nerves and veinlets immersed to somewhat prominulous beneath; inflorescences terminal, congested, appearing fundamentally cymose, invested with bracts and bracteoles, these conspicuous, puberulent on both surfaces, chartaceous; calyx limb with 5 essentially free lobes; corolla hypocrateriform, the tube elongate, the limb spreading, 5-lobed, the lobes sinistrorsely contorted in bud, entire; stamens 5, attached at corolla throat and alternate with lobes, the anthers exserted, subsessile, recurved, capped by the short apiculate connective, dehiscing longitudinally; hypanthium strongly 5-angled; ovary 2-celled, capped by a 2-lobed dome-shaped disk; ovules numerous, as many as one thousand in each locule, attached to an elongate central placenta; style filiform, the stigma exserted, clavate, bifid above middle; fruit an obovoid capsule surmounted by the persistent and narrowly decurrent calyx lobes, dehiscing septicidally along 2 sutures, the endocarp thin and bony; seeds small, essentially rhomboidal, the testa smooth.

The genus *Lindenia* was proposed by Bentham in *Plantae Hartwegianae* and was based on a K. T. Hartweg collection from Verapaz, Guatemala. Only one species, *L. rivalis*, was described; this is the type species. The name of this new American genus was first printed as *Siphonia*, but Bentham, shortly before the distribution of that fascicle of *Plantae Hartwegianae* (fascicle M, pp. 81–88), found that the generic name *Siphonia* had previously been employed in the Euphorbiaceae. Hooker (1873) and Standley (1921) have pointed out that the name *Lindenia* was holographically substituted in all copies of that fascicle of *Plantae Hartwegianae* before distribution, and their assumption that the name *Siphonia* was indeed scratched out in *all* copies is accepted here. In the copies consulted by me, this was found to be the case, and the effective publication of *Lindenia* by indelible autograph, as permitted by Article 29 of the *International Code of Botanical Nomenclature*, may be accepted. Standley (1921) suggested that there is no reason to cite "*Siphonia* Bentham" as a synonym of *Lindenia*, since the former name was never really published except as it has appeared in synonymy. However, if copies of *Plantae Hartwegianae* exist in which the name *Lindenia* was not substituted, then its effective publication on that date is questionable.[1] For this reason, *Siphonia* sensu Bentham is maintained in the present synonymy.

Even if *Lindenia* is not accepted as having been published by Bentham in 1841, it was described one year later by both Bentham and Endlicher. Their publications of *Lindenia* in the Rubiaceae predate the use of the same name by Martens and Galeotti in 1843 for a genus in the Nyctagi-

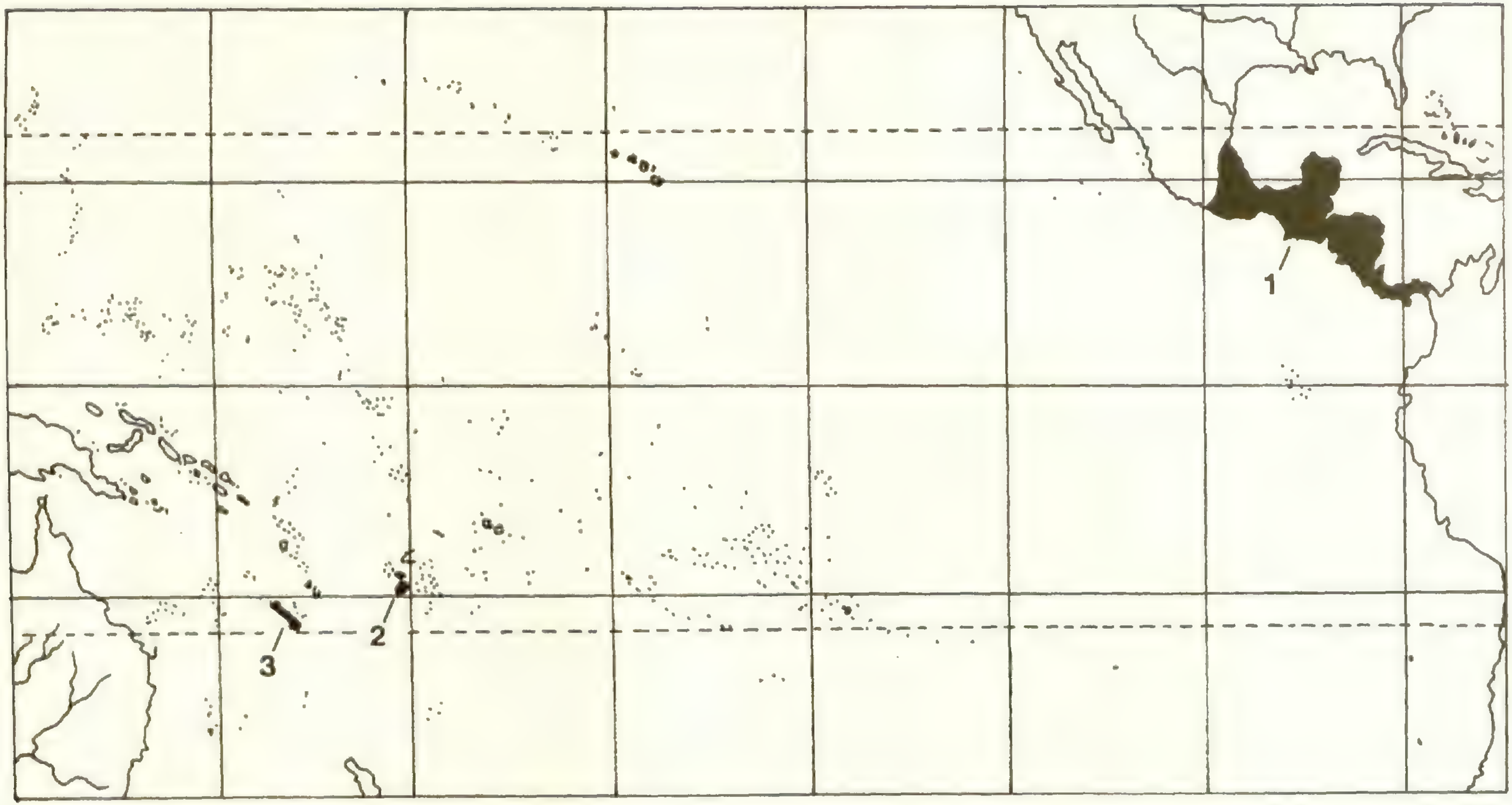
[1] It should be noted that in recent "facsimile" editions of *Plantae Hartwegianae* the handwritten name *Lindenia* has been removed and *Siphonia* restored.

naceae. The fascicle of *Plantae Hartwegianae* containing Bentham's printed correction of the name *Siphonia* to *Lindenia*, on page 351, did not appear until 1857.

As interpreted here, *Lindenia* comprises three species, *L. rivalis* Bentham (the type species), limited to tropical Central America, *L. vitiensis* Seem., endemic to Fiji, and *L. austro-caledonica* Brongn., endemic to New Caledonia (MAP 1). By previous authors the genus had been ascribed to the islands of Samoa and Tobago (Guppy, 1906; Hutchinson, 1969), but such reports are in error. *Lindenia* is most easily recognized by its exceptionally long corolla tubes, which are scarcely expanded at the throat (FIGURES 1, 13, 23). All of the species are characterized by occupying a strictly riverine habitat, or they are found growing in the middle of shallow watercourses.

Lindenia has been placed by all authors concerned with its taxonomy in the tribe Rondeletieae, and it agrees with other members of that tribe in a number of important characters. These include the capsular nature of the fruit (FIGURES 9, 10, 21, 31), the many ovules in each locule and their attachment to an elongate central placenta (FIGURES 6, 7), the nonalate seeds (FIGURES 11, 22, 32), the contorted aestivation of the corolla lobes (FIGURES 17, 27), and the subglobose, tricolporate pollen grains (FIGURES 8, 20, 30). Like other members of the Rondeletieae, *Lindenia* lacks raphid crystals, an important feature in the classification of the Rubiaceae according to Verdcourt (1958) and Bremekamp (1966). Significantly, *Lindenia* differs from certain other members of that tribe (*Rondeletia* in particular) by the contorted aestivation of its corolla. As usually interpreted, the tribe Rondeletieae contains genera with imbricate aestivation and genera with contorted aestivation. According to Bremekamp (1966), these two aestivation types are almost never encountered in closely related taxa, though imbricate and valvate aestivation are often closely associated. Further study may lead to the conclusion that the genera of the Rondeletieae with contorted corolla lobes should be removed from that tribe and placed elsewhere.

Although the association of *Lindenia* with the Rondeletieae may be uncertain, its closest relatives among extant genera are almost certainly American. Of the genera placed in the Rondeletieae by Schumann (1891), nearly all are American, and only a few extend into tropical and subtropical Asia. *Lindenia* is, however, the only member of the Rondeletieae with species indigenous in the Pacific. In general morphology, *Lindenia* approaches the Brazilian genus *Augusta* Pohl, but the latter genus, as pointed out by Bentham (1842), differs in its shorter, more expanded corolla tubes, shorter calyx lobes, more exserted stamens, axillary inflorescences, and loculicidally dehiscent fruits. A superficial resemblance is also shared between *Lindenia* and *Tocoyena* Aublet, a member of the Gardenieae. *Tocoyena*, however, with a baccate fruit and seeds embedded in a pulpy matrix, seems to be a firm member of the tribe Gardenieae and not closely related to *Lindenia*. A clarification of the relationships of *Lindenia* must await a detailed review of the tribe Rondeletieae.



MAP 1. Geographical distribution of *Lindenia* Bentham (Rubiaceae). 1 = *L. rivalis* Bentham; 2 = *L. vitiensis* Seem.; 3 = *L. austro-caledonica* Brongn.

The relationships of the Fijian flora are now fairly well known, owing primarily to the work of Dr. A. C. Smith. This flora is, in large part, derived from Indo-Malesian elements, and no transpacific migrations are thought to have been involved (Smith, 1955). The only exceptions to these observations occur in the predominantly American genera *Lindenia* and *Stillingia* L. (Euphorbiaceae). Similarly, *Lindenia* and *Epistephium* Kunth (Orchidaceae) form a puzzling American element in the New Caledonian flora (van Balgooy, 1971).

Concerning the widely disjunct distribution (MAP 1) of *Lindenia*, only two explanations seem possible. Either the disjunction is the result of chance long-distance dispersal, or the taxon was once continuous over an intervening land or insular area and has become restricted to now isolated populations. A third alternative, that human agency was involved, may definitely be excluded in the present case, since the New World and Old World portions of the genus have distinctive characteristics that could not have evolved in the immediate past.

There is little evidence to support the transpacific dispersal of *Lindenia* as an explanation of its present disjunct range. Although seeds of *Lindenia* are able to float in seawater by means of the crisp, air-filled outer tissues, it seems unlikely that these small seeds would be able to remain afloat for a sufficiently long time as to allow transportation over such a distance by ocean currents. Hypotheses have also been advanced (Guppy, 1906) that seeds of *Lindenia* may have become attached to the feet of migratory water fowl, but the smooth, rhomboidal seeds (FIGURES 11, 22, 32) show no obvious means by which they might become attached to the feet or plumage of such birds. Indeed, transpacific migrations must have been rare or nonexistent, since so few other genera have a pattern of disjunction like that of *Lindenia* (van Balgooy, 1971).

Unfortunately, nothing is known about the pollination biology of this genus. With such exceedingly long corolla tubes, it seems likely that flowers of *Lindenia* are visited by long-tongued lepidopterans. If such insects were at one time necessary for pollination in this genus, it seems unlikely that long-distance dispersal could have been possible without the concomitant dispersal of the required pollinators. However, certain moths already adapted to a pollination syndrome similar to that of *Lindenia* flowers may have been established in the Pacific before the arrival of *Lindenia* populations in Fiji or New Caledonia.

The most convincing argument against the transpacific dispersal of *Lindenia* is the fact that members of this genus are unknown from any intermediate archipelagoes. If its dispersal was the result of avian migrations, *Lindenia* might be expected to occur on other islands of the Pacific where appropriate habitats exist. Such, however, is not the case.

The hypothesis that *Lindenia* once occupied a much wider geographical area than it does today is more credible. It is easy to imagine that the small seeds were dispersed by wind, water, or even birds over short distances. After its origin somewhere on the American continent, *Lindenia* may have become established northward to Mexico and southward through

South America to the West Antarctic archipelago, and then westward to New Zealand, New Caledonia, Fiji, and possibly other islands of the southwestern Pacific, assuming that climatic conditions were favorable for such migration in the not too distant past. As mentioned above, all species of *Lindenia* are ecologically restricted to a habitat along the banks of rivers and streams. Such restriction was probably disadvantageous to *Lindenia* species as climatic changes and competition from other species were experienced. This strict habitat requirement, in conjunction with drastic climatic changes, was also probably in great part responsible for the extinction of *Lindenia* in South America, the West Antarctic archipelago, New Zealand, and other islands which at one time may have supported populations.

The Pacific and American species of *Lindenia* have so many characters in common, characters not shared with any other genus, that they seem to form a remarkably unified taxon in spite of their geographical disjunction. Such characters as the elongate, hypocrateriform corolla, the essentially free, subulate calyx lobes with glands near the base within, the frutescent habit, and the strict riparian habitat make *Lindenia* an easily recognized genus. It seems best, therefore, to maintain all three species within *Lindenia*, but to indicate their relationships by the recognition of two sections. As here interpreted, sectional distinctions are correlated with geographical distribution not because a long-distance-dispersed Pacific element was able to diverge rapidly from its American ancestor, but because the American and Pacific populations may represent the near-extreme ends of a once long, attenuate range. Divergence of the Pacific and American species would seem, therefore, to have been a slow process and the result of a gradual expansion of the area of *Lindenia* around the southern boundary of the Pacific. The similarity between the New Caledonian and Fijian species reflects their comparatively recent divergence at the younger end of this once continuous range.

Key to the sections

Stipules usually persistent, to 10 mm. long when mature, fused at base and forming a shallow cup surrounding the branchlet, gradually tapering toward apex into a sharply pointed acumen; style puberulent over basal half with thin, white, spreading hairs 0.3–0.7(–1.2) mm. long; valves of fruit often twisting strongly after dehiscence. . Sect. Lindenia.

Stipules caducous, 11–25 mm. long when mature, elliptic to lanceolate to oblanceolate, not obviously fused at base, acute to rounded at apex; style glabrous or with a few minute, scattered hairs about 0.1 mm. long; valves of fruit not twisting strongly after dehiscence. Sect. Pacifica.

Lindenia Bentham sect. Lindenia.

This, the first of the two sections here recognized, is monotypic, containing only the type species of the genus.

1. Lindenia rivalis Bentham, Pl. Hartweg. 84. 1841.

Shrub to 2 m. high, generally puberulent with white to stramineous hairs or glabrous, the branchlets subterete, 1.2–2.8 mm. in diameter toward apex, brown or often black, smooth or swollen at nodes; stipules usually persistent, interpetiolar, membranaceous, entire, to 10 mm. long when mature, fused at base and forming a shallow cup surrounding the branchlet, gradually tapering toward apex into a subulate acumen up to 5 mm. long, puberulent within and without with appressed, white to stramineous hairs up to 0.6 mm. long, these sometimes few and restricted to base or acumen or adaxial surface only; petioles stout, semiterete to canaliculate, 2–16 mm. long, 1.4–2 mm. broad; leaf blades lanceolate to elliptic to oblanceolate, 3.2–17.6 cm. long, 1–3(–4.2) cm. broad, the upper and lower surfaces glabrous to puberulent with scattered hairs, or these restricted to base and costa; domatia absent; inflorescences 1–7-flowered, the peduncle up to 1 cm. long or essentially none, the bracts usually trifid, 4.2–9.2 mm. long, 1.8–2.8 mm. broad at base, acuminate at apex, the bracteoles subulate to lanceolate, 1.5–6.8 mm. long, 0.5–1.2 mm. broad at base, acuminate at apex, the pedicels slender, 3.6–8.6 mm. long, gradually broadening into the hypanthium; calyx lobes subulate to linear-lanceolate, (7.6–)10–22 mm. long, 0.8–1.8(–2.8) mm. broad, usually acute to long-acuminate at apex, entire, chartaceous to subcoriaceous, puberulent on both surfaces with scattered, stramineous hairs about 0.2 mm. long, these longer and denser at base of lobes within and partially concealing as many as 20 reddish, multicellular glands, each up to 0.3 × 0.1 mm.; corolla tube (8–)10.2–16.4 cm. long, 1.4–2.6(–3.4) mm. broad at middle, puberulent to tomentose without with white to stramineous hairs up to 0.7 mm. long, glabrous within, the corolla limb spreading, 2.6–6.8(–8) cm. broad, the lobes ovate to elliptic to lanceolate, 12–32(–38) mm. long, 4.8–14(–16) mm. broad, rounded to acute to acuminate at apex, densely puberulent to somewhat strigillose within with scattered hairs up to 0.3 mm. long, densely puberulent to tomentose without; anthers oblong-linear, 8.6–11.8(–14.2) × 0.9–1.3 mm., glabrous to glabrescent with a few scattered hairs; hypanthium 4–8.5(–10) mm. long, 2.6–4.6 mm. broad at apex, usually densely puberulent with spreading, stramineous hairs up to 0.3 mm. long; style 10.6–15.4 cm. long, about 0.5 mm. broad, puberulent over lower half with spreading hairs 0.3–0.7 (–1.2) mm. long, the stigma 5.4–9(–12.5) × 0.8–1.8 mm., up to 6 mm. broad when the lobes are spread apart; fruits (14–)18–26.2 mm. long, 9–12 mm. broad, drying brown, becoming black, the valves obviously twisting after dehiscence, the endocarp thin and bony; seeds 1–1.5 mm. long, 0.5–1.4 mm. broad.

Although *Lindenia rivalis* is variable in many characters, two forms based on features of indument are recognizable and appear to be reasonably distinct.

Key to the forms of Lindenia rivalis

Indument consisting of white to stramineous hairs up to 0.6 mm. long variously present on young parts, branchlets, leaves, stipules, and inflorescences. ..... 1a. f. *rivalis*.

Indument restricted to inflorescences and adaxial surfaces of stipules; all other parts glabrous. ..... 1b. f. *glabra*.

1a. Lindenia rivalis f. rivalis. Figures 1–11.

Lindenia rivalis Bentham, Pl. Hartweg. 84. 1841, in Hooker's Icon. Pl. **5:** *t. 476.* 1842; Hooker in Bot. Mag. **87:** *t. 5258.* 1861; Hemsley, Biol. Centr.-Am. **2:** 26. 1881, in Ann. Mus. Nac. Rep. Costa Rica **1887**(2): 40. 1887; J. D. Smith, Enum. Pl. Guatemal. **2:** 30. 1891; Shannon in Intercont. Railway Commis. Rep. 1(2), Appendix **3:** 11. 1898; Pittier, Ens. Pl. Usual. Costa Rica, 109. 1908; Standley in N. Am. Fl. **32:** 92. 1921; Standley & Calderón, Lista Prelim. Pl. El Salvador, 210. 1925; Standley in Contr. U. S. Nat. Herb. **23:** 1358. 1926, in *op. cit.* **27:** 355. 1928; Standley & Record in Field Mus. Nat. Hist. Bot. Ser. **12:** 383. 1936, Standley in *op. cit.* **18:** 1325. 1938; Miranda, Veg. Chiapas Sec. Parte, 289. 1953; Pittier, Ens. Pl. Usual. Costa Rica, ed. *2.* 147. 1957; Porter in Graham, Veg. & Veg. Hist. N. Latin America, 192. 1973; Standley & Williams in Fieldiana **24**(11): 119, *fig. 6.* 1975.

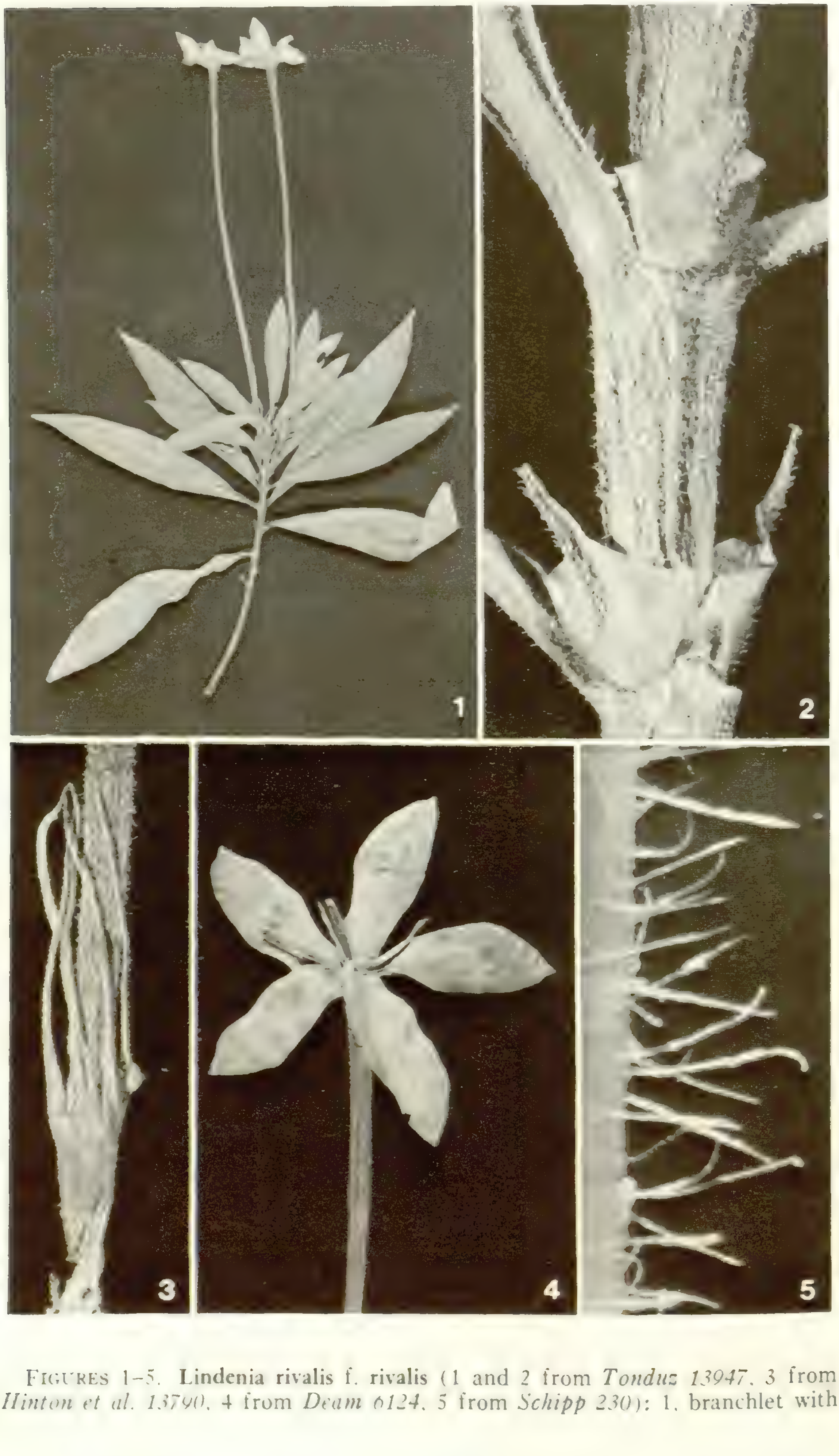
Siphonia rivalis Bentham, Pl. Hartweg. 84. 1841.

Lindenia acutiflora Bentham in Hooker's Icon. Pl. **5:** *t. 475.* 1842; Mart. & Gal. in Bull. Acad. Roy. Bruxelles **11:** 240. 1844; Hemsley, Biol. Centr.-Am. **2:** 26. 1881.

The typical form of *Lindenia rivalis* usually bears an obvious indument; at least the young parts, branchlets, leaves, and stipules are never glabrous all at the same time. The form includes nearly all of the neotropical collections of the genus.

Type locality. Bentham based the genus *Lindenia* solely on *Hartweg 581* from Guatemala, although Hooker was of the opinion that *L. rivalis* had been collected first by Linden on the banks of the Río Teapa, Mexico. One specimen, *Linden 331* (K), is labeled as having been collected at that locality in 1840, but since it was unmentioned in Bentham's original description, it cannot be considered a possible type of the species. Four examples of the Hartweg collection are known, two of these being at Kew. Only one of the two Kew specimens may be considered the holotype, the one bearing the stamp identifying it as having been a part of Bentham's own herbarium. The other Kew sheet was transferred from the Hooker herbarium in 1867. Only the "Bentham" sheet is labeled "Vera Paz, Guatemala" and bears the name "*Siphonia rivalis*."

The type of *Lindenia acutiflora* is *Linden 358*, the only collection cited by Bentham. This collection is known only from a single specimen at Kew labeled "Mexico. Vera Cruz. Puente nacional. 1838" and was originally part of the Hooker herbarium.



FIGURES 1–5. **Lindenia rivalis** f. **rivalis** (1 and 2 from *Tonduz 13947*, 3 from *Hinton et al. 13790*, 4 from *Deam 6124*, 5 from *Schipp 230*): 1, branchlet with

DISTRIBUTION. The typical form of *Lindenia rivalis* is restricted to tropical Central America and extends from northern Veracruz, Mexico, southward to Panama. It ranges in altitude from near sea level to 1500 m. Like other members of the genus, it is always found growing on the banks of rivers or, not uncommonly, directly in the waterways.

In habit, *Lindenia rivalis* f. *rivalis* is a shrub with leaves which are pale and silvery beneath. The plant is a showy one with long white corollas, these sometimes having a pinkish tube and white lobes. The flowers open in the morning and evening and are very fragrant. The fruits are also attractive; although at first green, they often become red and later brown. Flowering specimens of this form have been collected between April and July, rarely at other times of the year. Fruiting material is most commonly found between August and March.

LOCAL NAMES AND USE. The following names have been recorded: Mexico (Oaxaca), *pimenta de agua* (*Standley 1926*); Guatemala, *amalillo* (*Steyermark 42110*), *flore de Maria*, *mes-i-ha* (*Pittier 180*); Honduras, *chilca* (*Edwards 230*), *culebrita* (*Glassman 1553*), *lirio* (*Standley & Chacón 5606*); Costa Rica, *jarmincillo* (*Valerio 117*), *lirio de agua* (*Jimenez 507*); Panamá, *guabita de quebrada* (*Stern et al. 1788*). Herbarium specimens attest that this species was under cultivation as an ornamental shrub on the island of St. Vincent and at Kew in 1894. With its elongate, fragrant flowers and lush foliage, *Lindenia rivalis* probably has horticultural potential.

Mexico. MICHOACÁN: Pihuamo, *M. E. Jones 311* (MO, US); San José, Coalcomán, *Hinton et al. 13790* (F, GH, MO, NY, US); Las Minitas, Torrent de Chutá, *Langlassé 198* (GH, K, US). GUERRERO: Galeana, Atoyac, *Hinton et al. 14578* (K, NY, UC, US). OAXACA: Mogoñe, on F. C. N. T., *Orcutt 5206* (MO); Santo Domingo, *Nelson 2659* (GH, US); Paso Lagarto, Río Magdalena, Pochutla, *Conzatti, Reko, & Makrinius 3112* (GH). VERACRUZ: Río de los Pescados Baños del Carrizal, *Purpus 6099* (GH, MO, NY, UC); Colipa, *Karwinsky 1258* (F); Río Limón east of Paso de San Juan at Highway 140, *Maxwell 167* (MO); canyon 15 mi. southeast of Jalapa, *Barkley, Rowell, & Webster 2582* (F); Cavarrillo, *Pringle 8151* (AC, BM, F, GH, K, MO, NY, UC, US); Puente Nacional, *Linden 358* (K, holotype of *L. acutiflora*), *Purpus 13007* (F), *14240* (A, F); Barranca de Panoaya, *Purpus 8503* (UC); San Francisco, *C. L. Smith 1365* (F, NY, UC); vicinity of Veracruz, *Galeotti 1572* (K); Fortín, *Purpus 8483* (GH, MO, NY, UC, US); Orizaba, *Botteri* (GH); Cuitláhuac, *Matuda 1440* (A, K, MO, NY); Paso de Ingenio, *Calzada 323* (GH); Río de Santiago de Tuxtla, *Galeotti 2683C* (F); vicinity of Zacuapán, *Purpus 14270* (A, F); Los Tuxtlas, Ocotal, Chico, *Ross 208* (US); Dos Ríos, Río Grande de Cerro Gordo, *Ventura 2593* (NY); Paso del Correo, *Liebmann "Rubiaceae n. 5"* (*11419 or 11519*) (GH, K, MO, NY, US); Veracruz, without further locality, *Rosas 625* (A). TABASCO: Río Teapa, *Linden 331* (K). CHIAPAS: Sayula, *Juzepczuk 1353* (F); Javalinero, Palenque, Río Chacamax, *Matuda 3615* (A, F, K, NY); Río Despoblado near Comatitlán, *Matuda 17654* (F). MEXICO, uncertain locality ("Soledad"), *Wawra 156* (NY);

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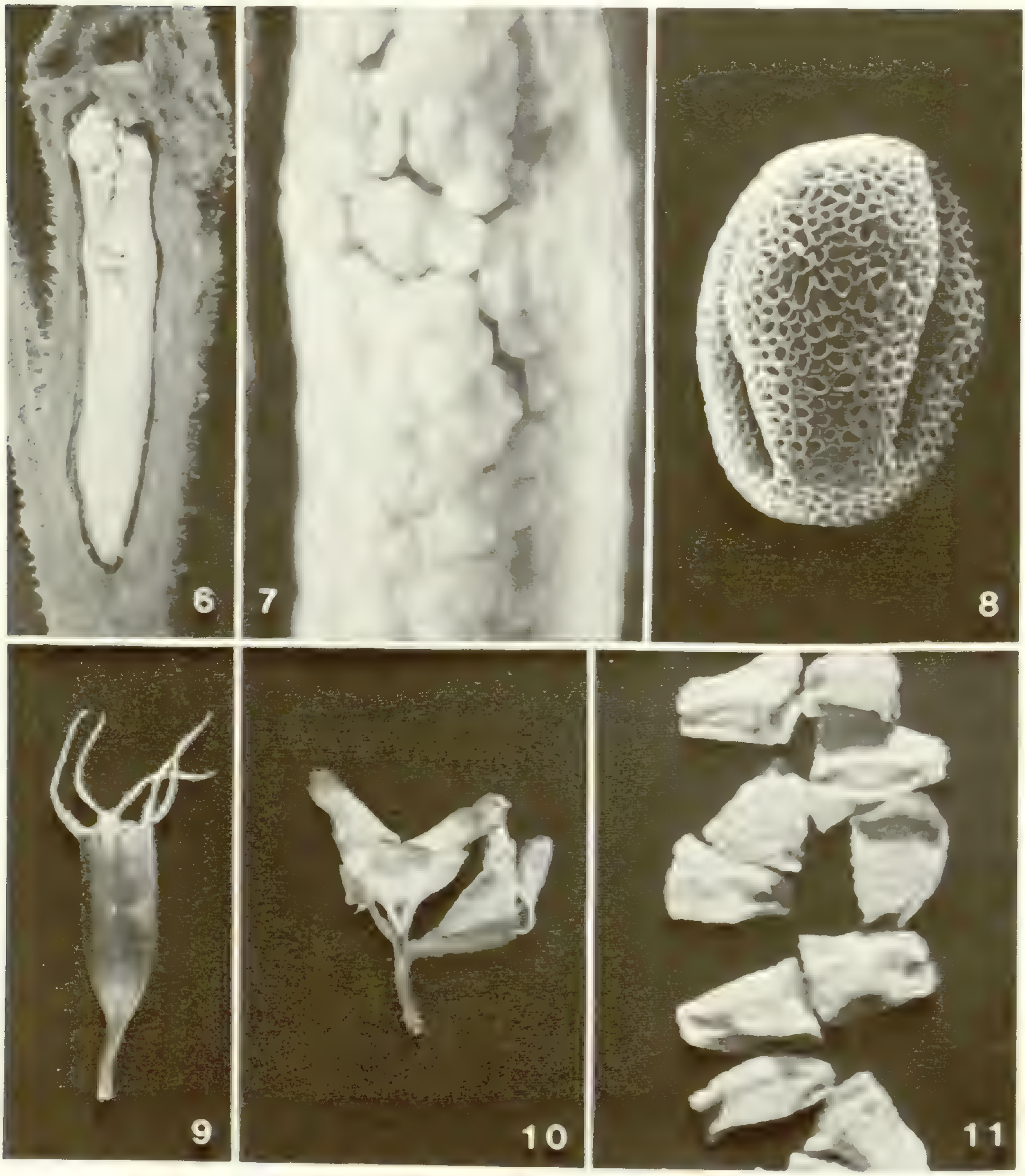
inflorescence, × 1/3; 2, branchlet showing stipules and petiole bases, × 4; 3, hypanthium, calyx, and base of corolla, × 2; 4, corolla limb with exserted stamens and stigma, × 1; 5, surface of style showing indument, × 40.



FIGURES 6–11. **Lindenia rivalis** f. **rivalis** (6 and 7 from *Calderon 2192*, 8 from *Pringle 8151*, 9 from *Lundell 6687*, 10 from *Bartlett 11767*, 11 from *Contreras 7047*): 6, longitudinal section of ovary showing elongate placenta, × 6; 7, portion of placenta showing ovules, × 30; 8, pollen grain, × 2000; 9, fruit prior to dehiscence, × 1; 10, dehisced fruit, × 1; 11, seeds, × 10.

without further locality, *Harris* (K), *"Herb. Pavon"* (BM), *Sartorius* (US). **Belize.** CAYO: Chiquibul Forest, east branch of Belize River at Guacamallo, *Brunt 2265A* (BM); between Benque Viejo and Melchor de Mencos, *Croat 24594* (MO); Río Mopan near Benque Viejo, 7 km. on Arenal Road, *Contreras 7047* (F, NY); vicinity of Cayo, *Lundell 6103* (F, GH, NY, US); vicinity of Vaca, *Gentle 2573* (A, F, K, MO); Mt. Pine Ridge, near Privation Creek, 12 mi. south of Cayo, *Burch 6255* (MO), Pinol Creek, *Proctor 30199* (BM), about 5 mi. south of Augustine Rd., 35 mi. south of San Diego, *Long 3237* (MO, NY), Río Frio, *Hunt 7063* (K), *Lundell 6687* (F, GH, NY, US); Mt. Pine Ridge, *Bartlett 11767*

(F, US); road to Augustine and San Luis, *Dwyer, Elias, & Maxwell 340* (MO); Hummingbird Highway, mi. 28, *Gentry 8587* (MO), mi. 30, *Gentry 8582* (MO), at Fairweather Creek, *Gentle 8833* (BM, F, NY, UC, US), at St. Margaret Creek, *Gentle 8722* (US); road to Church Yard, Beaver Dam Creek, *Campbell 109* (K); Big Creek, *Schipp 230* (A, BM, GH, K, MO, NY, UC, US). TOLEDO: Columbia Forest Station, *Dwyer 9846* (MO); San José, 1.5 mi. on road to Columbia Forest Station, *Gentry 8102* (MO); Moho River, *Peck 558* (GH, K); north side of Río Sarstún, *Harmon & Dwyer 2851* (MO). **Guatemala.** PETÉN: Dolores, 1 km. east of Río Ixcol, *Contreras 2409* (US). ALTA VERAPAZ: Chisaxte River below Secanquim, *Pittier 180* (US); vicinity of Finca Sepacuite, *Cook & Griggs 688* (US). BAJA VERAPAZ: 5 mi. southwest of Granados, *Harmon & Dwyer 3031* (NY); Verapaz, without further locality, *Hartweg 581* (K, holotype; isotypes at BM, K, NY). IZABAL: Jacoló, *H. Johnson 1137* (US); Lago Izabal between Punta dos Reales and Punta de Lechuga, *Steyermark 39616* (F); Montaña del Mico between mi. 49.5 and ridge 6 mi. from Izabal, *Steyermark 38603* (F); Río Oscuro, 0–8 km. southwest of Lake Izabal, *Jones & Facey 3492* (F, MO); Río Frio, *Steyermark 39921* (A, F, GH, NY). SAN MARCOS: Rodeo, Río Chol, *Lehmann 1452* (BM, F, US). RETALHULEU: Río Coyote, 4 km. west of Retalhuleu, *Standley 87425* (F, US), *87484* (F); road between Retalhuleu and Asintal, *Standley 87861* (F). QUICHÉ: without further locality, *Aguilar 1244* (F). ESCUINTLA: Río Michatoya, *J. D. Smith 2051* (GH, K, US), *Standley 89095* (F), *89103* (F); Río Guacalate, *Shannon 3646* (GH, US). ZACAPA: Río Teculután, *Steyermark 42110* (F). SUCHITEPÉQUEZ: vicinity of Santo Domingo south of Mazatenango, *Standley 88908* (F, US). Guatemala, uncertain locality ("Agua Calientes"), *Deam 6124* (GH, MO, US). **El Salvador.** SANTA ANA: Río del Molino, *Calderón 2192* (NY, US). LIBERTAD: La Libertad, *Barclay 1130* (BM, US); Libertad, without further locality, *Barclay* (K). SAN VICENTE: vicinity of San Vicente, *Standley 21218* (GH, NY, US), *Standley & Padilla 3394* (F). **Honduras.** COMAYAGUA: vicinity of Siguatepeque, *Rodriguez 2684* (F), *Standley & Chacón 6117* (F); Rancho Grande, San Luis, *Edwards 230* (A, F, US); vicinity of Comayagua, *Standley & Chacón 5606* (F). FRANCISCO MORAZÁN: Santa Clara Creek, *Williams & Molina 10071* (F, GH, UC), *10348* (F); drainage of Río Yeguare, *Williams & Molina 15863* (BM, F, GH, US), *Glassman 1553* (F); vicinity of Zamorano, *M. & J. Hernández 5122* (F), *Rodriguez 166* (F); Río de la Orilla, Cerro Majicaran, *Molina 106* (F, GH, MO, UC, US); Río de la Orilla southeast of Zamorano, *Standley 22110* (F); Quebrada el Horno between Frijolar and Tabla Grande, *Molina 847* (F, GH). EL PARAÍSO: Quebrada de Dantas, 12 km. northeast of Yuscaran, *Molina 10044* (F, US); Río Choluteca near Oja de Agua, *Standley 4682* (F); 5 km. east of Oja de Agua, *Standley 4686* (F); Montaña Teupasenti between El Junquillo & Teupasenti, *Molina 11890* (F, NY); Sierra de La Villa Santa above Jacaleapa, *Williams 18162* (F, GH, US). OLANCHO: Río Wampú, Mata de Tarro, 18 km. northeast of Pisijire, *Nelson & Clewell 696* (MO). HONDURAS, without further locality, *Shakespear* (BM). **Nicaragua.** CABO GRACIAS A DIOS: Mosquito Coast, *Schramm* in 1924 (US); Río Sangsang, *Schramm 15* (F, US). MATAGALPA: Río Las Cañas 15 km. northeast of Matagalpa, *Williams, Molina, et al. 27531* (F, GH, NY, US). GRANADA: vicinity of Nandaime, Río Ochomogo, *Lévy 20* (F). NICARAGUA, uncertain locality ("Embarquito, Nialyo"?), *Seemann 111* (BM). **Costa Rica.** GUANACASTE: Sapoá, *Ørsted 11520* (US); between Sapoá and Tortuga, *"70"* (K); Las Cañas road 5 km. southeast of Liberia, *Harris 53* (F); Palo Verde research area E, *Frankie 168* (F, MO); Finca La Pacifica, Río Corubici 6 km.

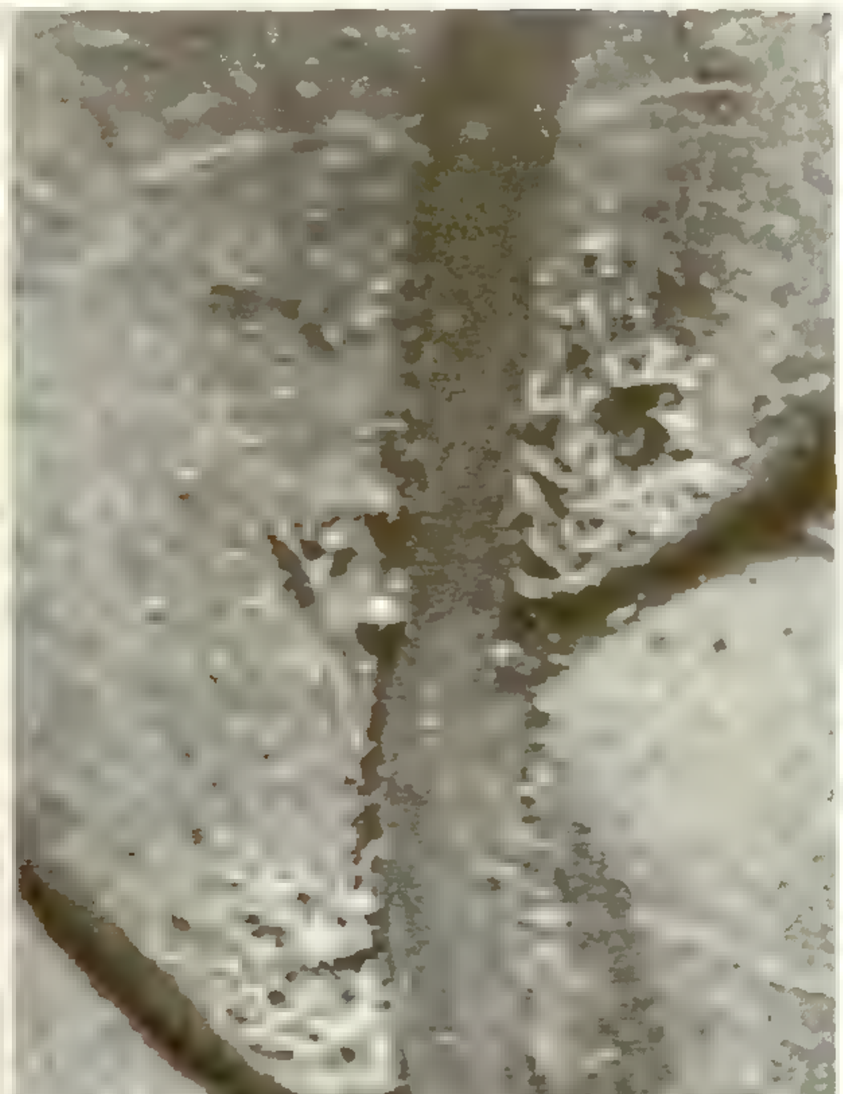


FIGURE 12. **Lindenia rivalis** f. **glabra:** branchlet with stipules and petiole bases, × 4, from *Steyermark 45966*. FIGURES 13–18. **Lindenia vitiensis** (13 from *Fiji*

northwest of Las Cañas, *Whitmore 20* (F, MO, NY); 22 km. along road to Finca Tenoria, *Croat 625* (MO); Hacienda Tenorio near La Pacifica, *Blum 366* (MO); Sandillal River north of Las Cañas, *Daubenmire 750* (F); Río Chiquito between Tilarán and Las Cañas, *Brenes 12702* (A, F, NY); vicinity of Tilarán, *Valerio 117* (US), *1144* (F), *Standley & Valerio 45678* (A, US); Nicoya, between Curime and Caimital, *Jimenez 507* (F); river at Nicoya, *Tonduz 13947* (BM, GH, K, US); La Colonia, Nicoya Peninsula, *Cook & Doyle 717* (US). PUNTARENAS: between Cascajal and Pigres, *Holm & Iltis 263* (BM, F, NY). **Panamá.** HERRERA: vicinity of Las Minas, Río Las Trancas, *Stern, Eyde, & Ayensu 1788* (MO, US). PANAMÁ: Río Bayano above confluence with Río Chepo, *Duke 3984* (MO); Chagres River, vicinity of Alhajuela, *Pittier 3521* (BM, GH, NY, US); Río Diablo, *Mayo 633* (MO); vicinity of Pacora, *Allen 3452* (BM, F, NY); upper Río Mamoni, *Pittier 4483* (BM, F, GH, NY, US); Río Canita near Jenine, *Duke 3842* (MO); Río Pasiga above waterfall on second main fork, *Gentry 2298* (MO); Río La Maestra, *Allen 24* (A, F); Utibé, *Maurice 759* (US). CANAL ZONE: Road K-6, east of Arriján, *Croat 15036* (GH, MO, NY); Road K-9, vicinity of Río Cocoli, *Stern, Chambers, Dwyer, & Ebinger 7* (GH, MO, UC, US); Road K-9, *Dwyer 3008* (MO); Río Aqua Salud between Frijoles and Pipeline Road, *Foster & Kiester 1951* (GH, NY). DARIÉN: Río Morti, Drill Site 7, *Duke 14208 (3)* (F, MO, NY). **Unknown locality.** "P. H. 23/8/12" (K). **Cultivated plants.** GUATEMALA: *"Stove — July — 1894"* (K). ST. VINCENT: cultivated shrub at Government House, *Powell 28* (K).

In the morphology of its vegetative and reproductive parts, the typical form of *Lindenia rivalis* is quite variable. Particularly noticeable is the range in the size and shape of the leaves and their indument, as well as the distribution of the leaves on the branchlets, i.e. whether they are crowded toward the tips of the branchlets or whether they are more equally spaced. Correlating with general robustness is the size of the inflorescences and the individual flowers. Bentham distinguished *L. acutiflora* from *L. rivalis* on the basis of such features, as well as the more densely pubescent lower surfaces of the leaves, the small size of the leaves, and the more acute apices of the corolla lobes. With many more collections now available for comparison, the type specimen of *L. acutiflora* readily falls within the continuum of variation ascribable to *L. rivalis* f. *rivalis* and cannot be satisfactorily separated from that taxon.

1b. Lindenia rivalis f. glabra S. Darwin, f. nov. FIGURE 12.

Lindenia rivalis sensu J. D. Smith, Enum. Pl. Guatemal. 3: 39. 1893; non Bentham.

Frutex idem ac forma typica sed indumenti restrictione ad inflorescentias et stipulae paginas interiores differt.

Dept. Agr. 2288, 14 from *Seemann 217*, 15 from *Fiji Dept. Agr. 2153*, 16, 17, and 18 from *Fiji Dept. Agr. 2288*): 13, branchlet with inflorescence, × 1/3; 14, abaxial surface of leaf blade showing axils of secondary nerves with domatia, × 10; 15, apex of branchlet showing stipule and young leaves, × 2; 16, hypanthium, calyx, and base of corolla, × 2; 17, corolla lobes in bud, × 2; 18, surface of style, × 40. (s = stipule.)

TYPE LOCALITY. Chicomucelo ("Chicomuselo"), Chiapas, Mexico; type, *Matuda 4449*.

DISTRIBUTION. This essentially glabrous form of *L. rivalis* is known from localities in Mexico, Guatemala, and Costa Rica. In its altitudinal range, habit, ecology, vegetative and floral morphology, and probable reproductive biology, the new form is similar to the typical form.

LOCAL NAMES AND USE. As far as is known, this taxon is not distinguished by Central Americans from *L. rivalis* f. *rivalis*, and the names and use ascribed to the typical form also pertain to f. *glabra*.

Mexico. TABASCO: Tenosique, *Matuda 3493* (A, F); Río Teapa (Río Morelia) at Teapa, *Gilly & Hernandez 273* (GH). CHIAPAS: Chicomucelo, *Matuda 4449* (US 2087017, holotype; isotypes at A, F, MO, NY); Santa Margarita, *Mell 2025* (NY, US); Chiapas, without further locality, *Ghiesbreght 860* (GH). **Guatemala.** PETÉN: Río Machaquila north of El Cambio, *Steyermark 45966* (F, US). QUEZALTENANGO: Río Ocosito, *Heyde & Lux 2753* (GH, K, MO, NY, US). **Costa Rica.** GUANACASTE: Los Conventillos, *Tonduz 2672* (US); vicinity of Las Cañas, Finca La Pacifica, Río Tenorio, *Daubenmire 647* (F); Finca La Pacifica, northwest of Las Cañas, Río Corobici, *Opler 945* (F, MO).

As stated above, *Lindenia rivalis* f. *glabra* is distinguished by the restriction of the indument to the inflorescences and inner surfaces of the stipules. Amid the wide range of variation encountered in the species as a whole, this feature may seem insignificant, but the glabrous specimens appear to be sufficiently distinct to warrant their recognition as comprising a separate form. In considering what rank to assign this taxon, one may note that the Mexican and Guatemalan collections come from a fairly discrete area within the range of the species as a whole, but the occurrence of essentially identical plants in Costa Rica suggests that the glabrous condition is likely to be encountered throughout the range of the species. Therefore, the rank of *forma* seems more logical than the rank of *varietas*, which might imply a degree of geographic isolation.

Lindenia Bentham sect. **Pacifica** S. Darwin, sect. nov.

Frutices stipulis caducis, demum 11–25 mm. longis, ellipticis vel oblanceolatis, basim versus non manifeste connatis, ad apicem acutis vel rotundatis; stylo glabro vel cum pilis paucis et dispersis plus minusve 0.1 mm. longis; fructu post dehiscentiam non valde torto.

Of the two species placed in *Lindenia* sect. PACIFICA, the Fijian species, *Lindenia vitiensis* Seem., is designated the type.

KEY TO THE SPECIES OF SECT. PACIFICA

Domatia consisting of tufts of stiff hairs always present on the lower surface of leaf blades in axils of secondary nerves; inflorescences 13- or 14-flowered; interior of corolla tube puberulent with scattered hairs; corolla lobes

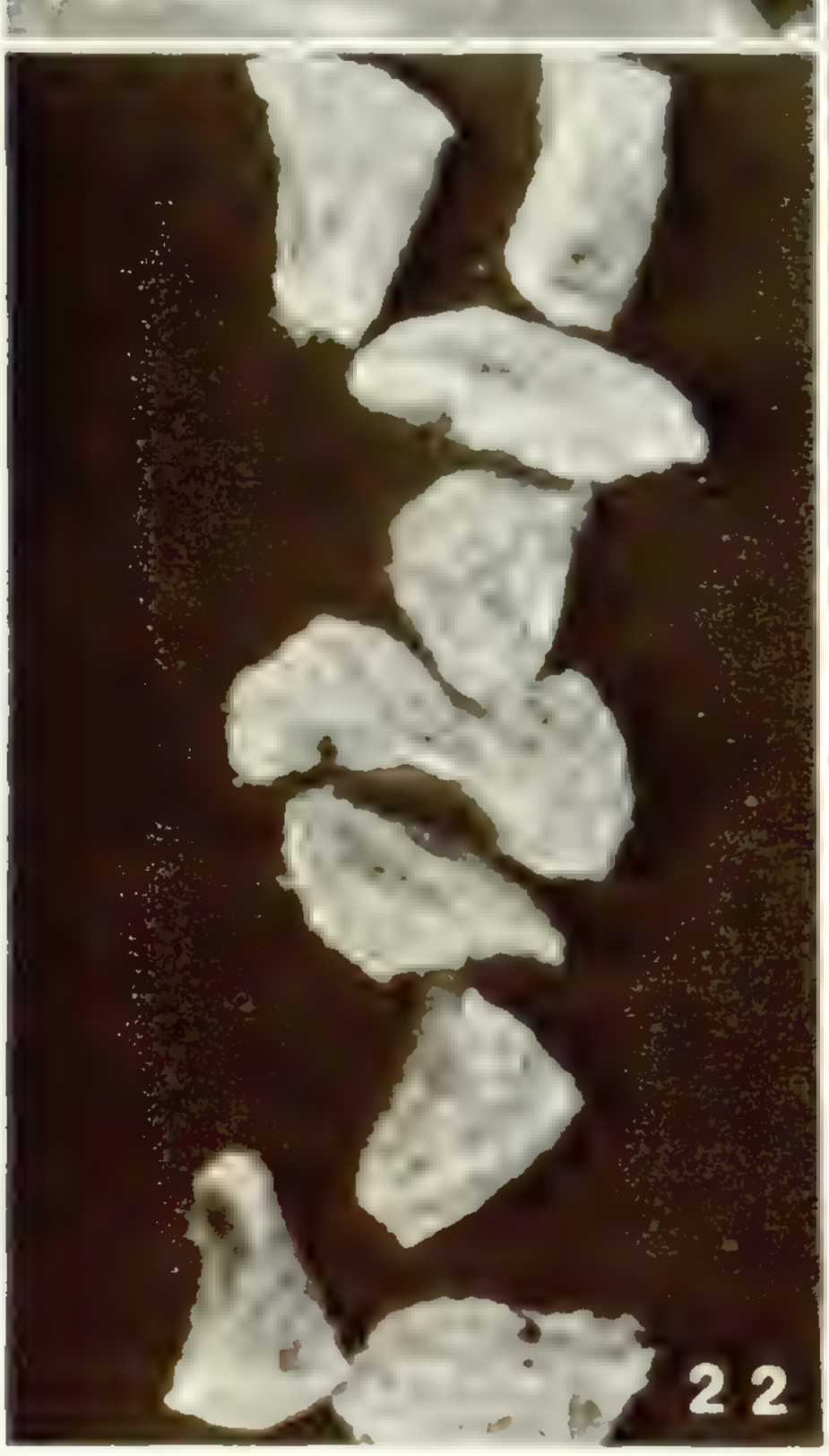
acute at apex; stipules usually more than 4.5 mm. broad when mature. . . . . 2. *L. vitiensis*.

Domatia rarely present on the lower surface of leaf blades; inflorescences 1–9-flowered; interior of corolla tube glabrous; corolla lobes sharply acute to acuminate at apex; stipules usually not more than 4.5 mm. broad when mature. . . . . 3. *L. austro-caledonica*.

2. **Lindenia vitiensis** Seem. in Bonplandia 9: 256. 1861. *nomen nudum*; A. Gray in Proc. Am. Acad. Arts 5: 318. 1862 (Jan.). *nomen nudum*; Seem. in Bonplandia 10: 33. *t. 8*. 1862 (Feb. 15); A. Gray in Bonplandia 10: 36. 1862; Seem. Viti, 438. 1862, Fl. Vit. 128. *pl. 24*. 1866, *op. cit.* 430. 1873; Drake, Ill. Fl. Ins. Mar. Pac. 186. 1890; A. C. Smith in Jour. Arnold Arb. 36: 288. 1955; J. W. Parham, Pl. Fiji Islands, 195. *fig. 71*. 1964, ed. 2. 276. *fig. 83*. 1972.

FIGURES 13–22.

Riverine shrub to 2 m. high, glabrous apart from the puberulent young parts and inflorescences, the branchlets subterete, 2.6–4.5 mm. in diameter toward apex; stipules soon caducous, interpetiolar, elliptic to oblanceolate, entire, 11–25 × 4.7–5.5 mm. when mature, broadly cuneate at base, obtuse to rounded at apex, finely puberulent with scattered hairs up to 0.2 mm. long or these slightly longer and persistent on branchlets above stipule scar; petioles stout, semiterete or canaliculate, 3–13 mm. long, 1.2–2.7 mm. broad; leaf blades lanceolate to narrowly elliptic, (6–)11–16 cm. long, (1.4–)2–3.8 cm. broad; domatia present, conspicuous on lower surface of leaf blades in axils of secondary nerves as tufts of stiff hairs 0.1–0.3 mm. long; inflorescences usually 3-branched, 13- or 14-flowered, the peduncle up to 1 cm. long or essentially none, the bracts usually paired at each node, trifid or divided to base and appearing whorled, 5.2–12.2 mm. long, 1–2 mm. broad at base, acute to acuminate at apex, the bracteoles undivided, linear-lanceolate to subulate, 2.8–8.1 mm. long, 0.3–1 mm. broad at base, acute to acuminate at apex, the pedicels slender, 1.2–2 cm. long and gradually broadening into hypanthium; calyx lobes subulate, 8–16 mm. long, 0.7–1.5 mm. broad at base, acuminate at apex, entire, chartaceous to subcoriaceous, puberulent without with hairs up to 0.1 mm. long and slightly longer ones within partially concealing as many as 10 yellowish, multicellular glands 0.2 × 0.1 mm. at base of each lobe, or glands absent; corolla tube 9.3–10.5 cm. long, 1.6–2.3 mm. broad at middle, puberulent without with hairs up to 0.2 mm. long, these more scattered within, the corolla limb 3–3.3 cm. broad, the lobes entire, ovate, 12–17 mm. long, 5–10 mm. broad, acute at apex, puberulent to tomentose within with densely matted, tangled hairs, densely puberulent without; anthers oblong, about 6 × 1.2–1.7 mm., glabrous; hypanthium 10–14 mm. long, 2.5–4 mm. broad at apex, strongly 5-angled, puberulent with short white to stramineous hairs; style 10–10.5 cm. long, about 0.5 mm. broad, glabrous or with occasional scattered hairs up to 0.1 mm. long, the stigma 3.2–4.1 × 1–1.6 mm., essentially glabrous; fruits 22–28 mm.



FIGURES 19–22. **Lindenia vitiensis** (19 and 20 from *Seemann 217*, 21 and 22 from *Horne 186*): 19, longitudinal section of corolla tube showing inner (left) and outer (right) indument, × 70; 20, pollen grain, × 2000; 21, fruit prior to dehiscence, × 1; 22, seeds, × 10. FIGURE 23. **Lindenia austro-caledonica:** branchlet with inflorescence, × $\frac{1}{3}$, from *Buchholz 1290*.

long, 8–11 mm. broad, drying brown, becoming black, the valves not obviously twisting after dehiscence; seeds about 1.5 × 1 mm.

TYPE LOCALITY. Seemann's original description of *Lindenia vitiensis* was based entirely on his own collection, *Seemann 217*. The species was reported to occur on the islands of Ovalau and Viti Levu, but the holotype bears only the notation "Navua River," which is probably the correct locality of the type collection. It is possible that Seemann observed this species growing on Ovalau, although no collection of *L. vitiensis* can be unequivocally assigned to that island. The isotypes are labeled "Viti or Fiji Islands," without further locality.

DISTRIBUTION. Judging from the comparatively few collections available, *Lindenia vitiensis* is a relatively rare species known with certainty only from the islands of Viti Levu and Vanua Levu. It is found growing in forests from near sea level to an altitude of about 100 m. and, significantly, always along the banks of streams. Its habit is that of a shrub up to 2 m. high with sweet-scented, cream-colored flowers. Flowering specimens have been collected in December, fruiting material in March.

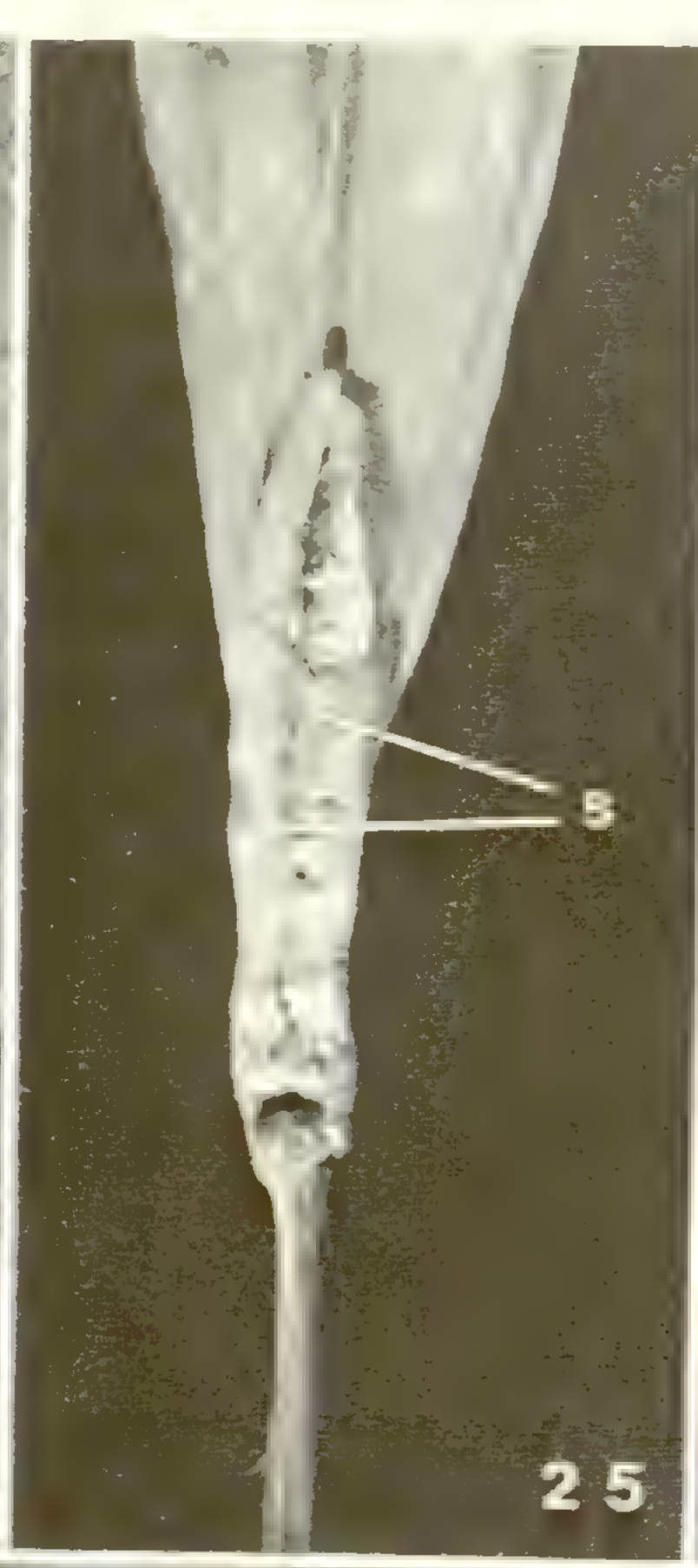
A single Graeffe collection of *Lindenia vitiensis* bears "Samoa" as a locality, but this species is otherwise unknown in that archipelago. It is likely that this Graeffe collection was mislabeled and is really of Fijian origin. Graeffe collected in southeastern Viti Levu, and in several other instances it is reasonably certain that specimens labeled "Samoa" actually came from Fiji (A. C. Smith, pers. comm.).

LOCAL NAMES. Seemann records the name *mbore ni wai*, a reference to the riverine habitat of this species. Variations include *mborewai* (*Fiji Dept. Agr. 2153*), *mbuarewai* (*Fiji Dept. Agr. 2288*), *mborewa*, and *mbua-siu*, the last two variants having been noted by Parham in the citations listed above.

Fiji. Viti Levu. SERUA: Navua River, *Seemann 217* (K, holotype; isotypes at BM, GH). NAITASIRI: Ndrauniwalai, Waindina River, *Fiji Dept. Agr. 1811* (BISH, SUVA), *2153* (BISH, K, MASS, SUVA, US). VITI LEVU, without further locality, *Graeffe* (K). **Vanua Levu.** MBUA: Nakorotiki, *Fiji Dept. Agr. 2288* (BISH, MASS, SUVA). FIJI, without further locality, *Horne 186* (K), *964* (GH, K). **Uncertain locality** ("Samoa"). *Graeffe* (BM).

The morphology of the stipules (FIGURE 15), the lack of a pronounced stylar indument (FIGURE 18), and the finely reticulate tectum of the pollen grains (FIGURE 20) indicate that this taxon is much more closely related to the New Caledonian species than to the American one. Seemann (1862) originally distinguished the Fijian species from *Lindenia rivalis* by the lack of pubescence on the lower surfaces of the leaf blades and by minute characters of the calyx lobes. Evidently he was unaware that the caducous stipules of *L. vitiensis* differ strongly from those of *L. rivalis*.

From *Lindenia austro-caledonica* the Fijian species is distinguished by the presence of domatia (FIGURE 14) on the lower surfaces of the leaf blades in the axils of the secondary nerves and by the blunter apices of the corolla lobes (FIGURE 17), a feature most easily seen when the flowers are in bud. In addition, the interior of the corolla tube (FIGURE 19)



FIGURES 24–29. **Lindenia austro-caledonica** (24 from *Schlechter 14992*, 25 from *C.B.I.B.S. 991*, 26 and 27 from *Buchholz 1290*, 28 and 29 from *Green*

is puberulent with scattered hairs in *L. vitiensis*, while it is glabrous in *L. austro-caledonica*.

3. **Lindenia austro-caledonica** Brongn. in Bull. Soc. Bot. France 12: 407. 1865. FIGURES 23–32.

Lindenia vitiensis sensu Brongn. & Gris in Ann. Sci. Nat. Bot. V. **6:** 258. 1866; Zahlbruckner in Ann. K. K. Naturhist. Hofmus. **3:** 280. 1888; Guillaumin in Ann. Mus. Colon. Marseille II. **9:** 168. 1911; Schinz & Guillaumin in Sarasin & Roux, Nova Caledonia Bot. 234. 1921; Däniker in Mitt. Bot. Mus. Univ. Zürich **142:** 442. 1943; Guillaumin in Bull. Soc. Bot. France **91:** 12. 1944, Fl. Nouv.-Caled. 328. 1948, in Bull. Mus. Hist. Nat. (Paris) II. **21:** 118. 1949; non Seem.

Riverine shrub to 3 m. high, glabrous apart from the puberulent young parts and inflorescences, the branchlets subterete, 2.5–4.3 mm. in diameter toward apex; stipules caducous, interpetiolar, elliptic to lanceolate, entire, 13–22.6 × 1.2–4.5 mm. when mature, broadly cuneate at base or occasionally fused for about one-third their length and forming a sheath around the branchlet, acute to rounded at apex, finely puberulent with hairs up to 0.1 mm. long or these slightly longer and persistent on branchlets above the stipule scar; petioles stout, semiterete or canaliculate, 3–16 mm. long, 1.4–2.4 mm. broad; leaf blades lanceolate to narrowly elliptic to oblanceolate, (3.5–)7–14.8 cm. long, (0.7–)1.4–3.9 cm. broad; domatia only rarely present on lower surface of leaf blades in axils of secondary nerves as tufts of stiff hairs 0.1–0.3 mm. long; inflorescences usually 2- or 3-branched, 1–9-flowered, the peduncle up to 1.5 cm. long or essentially none, the bracts often paired at each node, somewhat to conspicuously trifid, 5.8–12.5 mm. long, 1.2–4.5 mm. broad at base, acute to acuminate at apex, the bracteoles undivided, subulate, 1.8–9.2 mm. long, 0.7–1.8 mm. broad at base, acute to acuminate at apex, the pedicels slender, 1.2–3 cm. long and gradually broadening into hypanthium; calyx lobes subulate, 9–15(–19) mm. long, 1–2.2 mm. broad at base, acuminate at apex, entire, chartaceous to subcoriaceous, finely puberulent without with hairs about 0.1 mm. long or glabrous, densely puberulent within with hairs up to 0.3 mm. long and partially concealing as many as 10 yellowish, multicellular glands about 0.2 × 0.1 mm. at the base of each lobe, or such glands absent; corolla tube 8.6–11.7(–12.3) cm. long, 1.4–2.5 mm. broad at middle, very finely puberulent without with hairs up to 0.1 mm. long, glabrous within, the corolla limb spreading, 2.9–5.3 cm. broad, the lobes oblong-elliptic to ovate, 15–27 mm. long, 4.2–10 mm. broad, sharply acute to acuminate at apex, densely puberulent to tomentose with matted, tangled hairs within, more finely puberulent without;

1317): 24, abaxial surface of leaf blade showing axils of secondary nerves, × 10; 25, apex of branchlet showing pair of stipules and basal portion of a young leaf, × 2; 26, hypanthium, calyx, and base of corolla, × 2; 27, corolla lobes in bud, × 2; 28, longitudinal section of corolla tube showing glabrous inner surface (left) and outer indument (right), × 70; 29, surface of style, × 40. (s = stipule.)

anthers oblong, 5.3–8 × 0.9–1.4 mm., glabrous; hypanthium 10–16 mm. long, 2.7–4.2 mm. broad at apex, puberulent with short white hairs; style 9.2–11.7 cm. long, about 0.5 mm. broad, glabrous, the stigma 2.5–5.4 × 1.2–1.8 mm., essentially glabrous or with minute, glandular hairs; fruits 20–32 mm. long, 8–10 mm. broad, drying dark brown, becoming black, not obviously twisting after dehiscence; seeds about 1–1.5 × 1–1.5 mm.

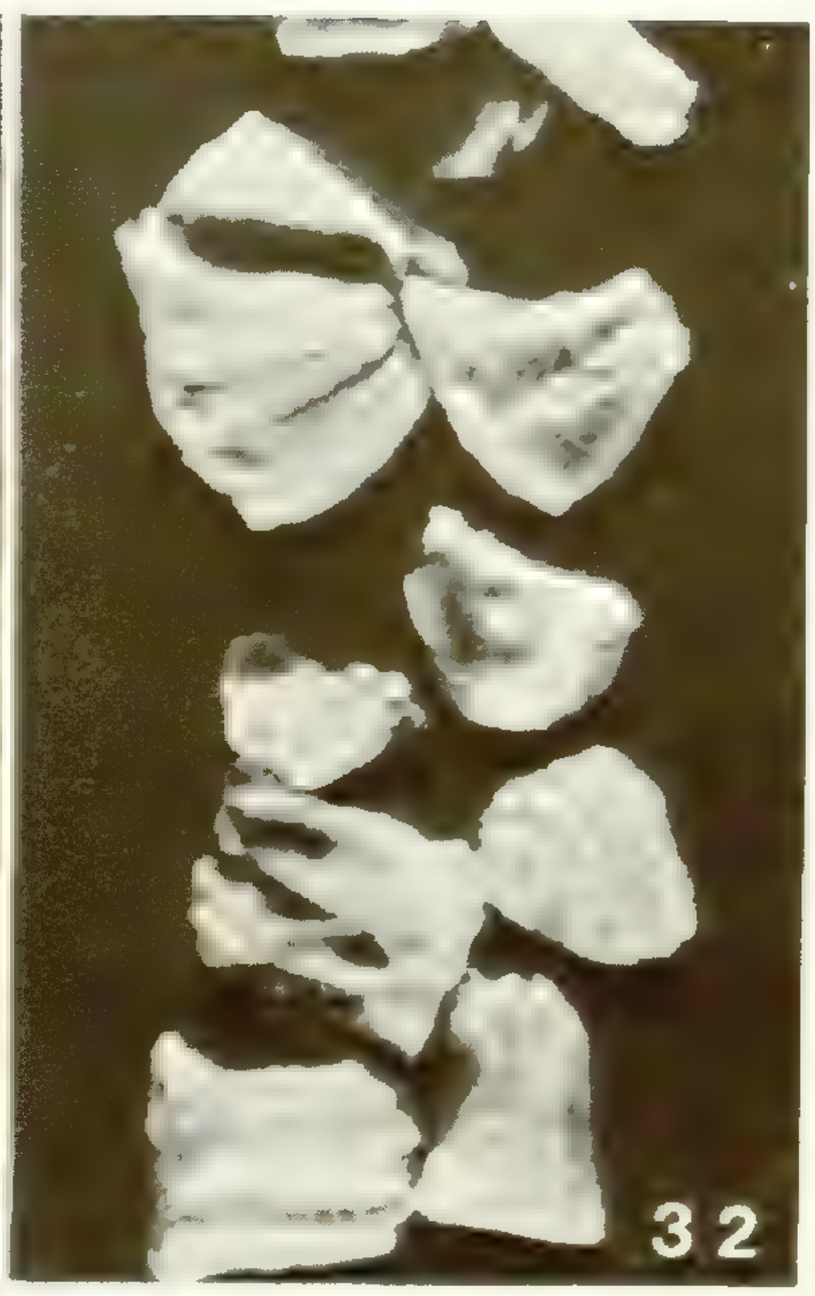
TYPE LOCALITY. Brongniart based *Lindenia austro-caledonica* on two collections which he cited as "habitat ad ripas rivorum Novae Caledoniae (Pancher, 1862); circa *Balade* (Vieillard, no. 651)." Of these two collections, specimens labeled *Vieillard 651* have been found scattered in European and American herbaria. It is important to note, however, that only two sheets (at K and P) are labeled as coming from the Balade locality cited by Brongniart. The remainder are labeled as having been collected at Wagap. In addition, the Balade sheets have the date "1855–1860" printed on their labels, whereas the Wagap labels read "1861–1867." It is probable, therefore, that *Vieillard 651* represents a mixed collection, the material having been gathered at different places and at different times. Evidently only the "Balade" specimens were available to Brongniart in 1865; these bear intact fruits, but the flowering material is poor.

The material collected by Pancher in 1862 is known definitely only from a single sheet (P), but because it consists of intact flowers as well as dehisced fruits, it seems the most appropriate lectotype and is here designated as such. Pancher's field label reads "Ourail — near (?) Kanala." Other Pancher specimens (at BM and K) are probably isolectotypes, although they are without collector's number and date.

DISTRIBUTION. Endemic to New Caledonia, but occurring throughout that island at elevations from sea level to about 375 m. Like the other taxa of *Lindenia*, this species is a shrub restricted to a riverine habitat. Flowering specimens have been collected between June and November; fruiting material has been found throughout the year.

New Caledonia. KOUMAC: Rt. 7, 16 km. north-northeast of Koumac, *Thorne 28117* (GH); road from Koumac to Balade, ascending first range of hills, *Green 1317* (A, K); 5 km. from Koumac on road to Ouégoa, *McKee 4715* (A, K). POUÉBO: Balade, *Vieillard 651*, 1855–60 (K, P); vicinity of Pouébo west of Colnett, near coast, *Webster & Hildreth 14804* (BISH). POINDIMIÉ: Wagap, *Vieillard 651*, 1861–67, (BM, F, GH, K, NY, P). CANALA: Canala, *Pancher* in 1862 (P, lectotype; probable isolectotypes at BM, K). MOINDOU: tributary of Rivière Boguen above waterfall at Tribu Katrikoin village on trail to Table Unio, *Buchholz 1290* (A, BISH, K, NY, UC, US). BOULOUPARI: Rivière Tahine, *Compton 1978* (BM). PAÏTA: mountains near Païta, *Schlechter 14992* (BM, K). DUMBÉA: Dumbéa Valley, north branch near river, *McKee 2480* (UC, US); Rivière Nondoué near airport, *Virot 312* (A); Rivière Nondoué, *Franc 629* (A, BM, K, NY, UC, US). NOUMÉA: near Nouméa, *Caldwell* (K). NEW CALEDONIA, without further locality, *C.B.I.B.S. 991* (K).

Brongniart, in the original description of this species, did not contrast it with the Fijian species which had been described by Seemann some



FIGURES 30–32. **Lindenia austro-caledonica** (30 from *Franc 629*, 31 from *McKee 2480*, 32 from *Vieillard 651* (1855–1860)): 30, pollen grain, × 2000; 31, dehisced fruit, × 1; 32, seeds, × 10.

three years earlier. Nor did Brongniart and Gris give any reason for the reduction of *Lindenia austro-caledonica* to *L. vitiensis* only one year after the publication of the former. As far as is known, all later authors have followed their example in considering the New Caledonian and Fijian *Lindeniae* as conspecific.

In fact, the magnitude of the differences between the two elements warrants the reinstatement of *Lindenia austro-caledonica* as a distinct species. The usual absence of domatia (FIGURE 24) in the New Caledonian species *versus* their presence in *L. vitiensis* is the most striking feature, although the occasional occurrence of domatia in New Caledonian plants may indicate that the presence or absence of domatia reflects the distribution of the presumed arachnid inhabitors rather than a genetic difference between the plant populations. However, the correlation of the usual absence of domatia in *L. austro-caledonica* with the glabrous interior of the corolla tube (FIGURE 28), the more acute corolla lobes (FIGURE 27), and the smaller stipules supports the conclusion that the New Caledonian and Fijian populations have diverged over a long period of time and should be considered distinct species.

EXCLUDED SPECIES

Lindenia acuminatissima Wernham in Jour. Bot. **52**: 227. 1914.

TYPE LOCALITY. Unknown.

Wernham based this species on a single specimen (K), which remains the only known collection. The type specimen bears a superficial resemblance to *Lindenia rivalis* in its somewhat elongate corolla tube and

sharply acuminate stipules, but in other characters it is quite different. Its corolla tube is not nearly as long as in true *Lindeniae*, and the calyx consists of six unequal lobes which are fused at the base into a distinct tube. The pubescence is also entirely different in that the hairs are much longer and stiffer. Wernham reported that the flowers are axillary, but in fact they are solitary and terminal on short axillary branchlets.

Although the limits of *Lindenia* might be extended to include Wernham's species, *Lindenia* is a much more uniform taxon if *L. acuminatissima* is excluded. The true taxonomic position of this collection is uncertain, and proper determination is difficult since its place of origin is unknown. The single specimen bears the notation "Gardenia mitis. Tobago Jasmine. Herb. Brown. (Barclay)?" The common name "Tobago Jasmine" hardly seems to be evidence that this plant was collected on the island of Tobago, and evidently there is also uncertainty as to whether or not it is a Barclay collection. Even if collected by Barclay, it may not be of Central American origin. Until more collections are available, it seems best to exclude this species from *Lindenia*.

Lindenia radicans Wernham in Jour. Bot. **52**: 226. 1914.

TYPE LOCALITY. This species is known only from the single type specimen, a Hartweg collection (K) made in 1839 but without a number. The holotype is labeled as having been collected at "Tocotepeque," Mexico; McVaugh (1970) has identified that locality as Jocotepec in the state of Oaxaca.

From other species of *Lindenia* this species differs in its long-petiolate, membranaceous leaves with much more broadly elliptic blades, the insertion of the anthers well within the corolla tube, the 4-parted corolla with a shorter tube, the unequal calyx lobes which may vary in number, and the much coarser indument consisting of longer, stiffer hairs. Unlike true *Lindeniae*, *L. radicans* is a recumbent shrub or woody vine. Wernham reported that elongate cystoliths are present in the membranaceous leaf blades. These are, however, the raised veinlets which give a rough texture to the surfaces of the leaves.

In the shape of the corolla and leaves, as well as in indument, *Lindenia radicans* is somewhat similar to *Tocoyena hirsuta* DC. from Brazil. In the latter species, however, the calyx is smaller and cupular. Until more collections are at hand, the position of this species cannot be assigned with certainty and it is best excluded from *Lindenia*.

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A MONOGRAPH OF THE GENUS PROSOPIS (LEGUMINOSAE SUBFAM. MIMOSOIDEAE)*

ARTURO BURKART

CATALOGUE OF THE RECOGNIZED SPECIES OF PROSOPIS[1]

(An enumeration with critical notes, citations of selected specimens,[2] descriptions, synonymies, distributions, ecologies, discussions of economic importance, and various other observations.)

Sect. PROSOPIS

1. **Prosopis cineraria** (L.) Druce. Rep. Bot. Soc. Exch. Cl. Brit. Isles 1913, 3: 422. 1914 (see Index Kewensis Suppl. 5. 1921); Burkart, Darwiniana 4: 61. 1940; Macbride, Contr. Gray Herb. 59: 16. 1919. BASIONYM: *Mimosa cineraria* Linnaeus, Sp. Pl. ed. 2. 2: 1500. 1763, excl. ref. Brown.

Prosopis spicigera Linnaeus, Mantissa Pl. 68. 1767; DC. Prodr. 2: 446. 1825.
Prosopis spicata Burmann, Fl. Indica 102. 1768, according to Index Kewensis and Macbride, *op. cit.*

ILLUSTRATIONS. Lamarck, Tabl. Encycl. 2: 340. 1797; Brandis, Illustr. Fl. N. West and Central India. *t. 25.* 1874.

Trees to 6.5 m. high; cortex cinereous; prickles internodal, scattered, straight, somewhat acroscopic, conical with broad bases. Leaves 1–3-jugate, glabrous or puberulous; petiole and rachis 0.5–4 cm. long, the pinnae 2–7 cm. long; leaflets 7–14-jugate, ovate, straight to subfalcate, without nerves (or 2–4-nerved at base, the midrib excentric), mucronate, 4–15 mm. long × 2–4.5 mm. broad, grayish when dry; stipules foliaceous, deciduous. Racemes spiciform, 5–13 cm. long, several together, subpaniculate; peduncle with amplexicaul bract (or 2 bracts united), this caducous and leaving an oblique scar, 1.5–2 mm. long; bractlets ovate, sessile, 0.5–0.8 mm. long, caducous; pedicels 0.5 mm., to 1.5 mm. long when mature; flowers yellow, glabrous; calyx truncate, 0.8–1.2 mm. long; corolla 3.5 mm. long, glabrous, the petals rolled back in age; anthers 0.8–1 mm. long; pistil glabrous. Fruit slender, elongate, 8–19 cm. long

* Continued from Volume 57, page 249.

[1] Herbarium acronyms indicating the location of cited specimens follow those cited in *Index Herbariorum* (ed. 6, 1974, compiled by P. K. Holmgren and W. Keuken, General Editor, F. A. Stafleu, Reg. Veg. **52**).

[2] Herbarium specimens cited in an earlier paper of mine, "Materiales para una monografía del género *Prosopis* (Leguminosae)," Darwiniana **4**: 57–128. 1940, are not included in the present lists of exsiccatae, except when necessary for correction or revision.

FIGURE 1. **Prosopis.** Left: Fruiting specimen of *P. cineraria* (*Wight 877*) (GH). Right: Fruiting specimen of *P. palmeri* (*I. L. Wiggins 5486*) from Baja California, Mexico (GH); flowering specimen, on same sheet, (*B. J. Hammerly 423*) from Baja California, Mexico (GH).

(including the stipe 0.8–2 cm.), subcylindric-torulose, 4–7 mm. in diameter, glabrous; pericarp thin, brittle; endocarp segments thin, longitudinal, little developed; seeds distant, longitudinal, ovate, 6 mm. long, the tegument with open horse-shoe fissural line on faces.

COMMON NAMES. Jand (Punjab); Ghāf (Arabia); Shumi (India, *fide* DC., 1825); and Jandi (Pakistan).

SELECTED SPECIMENS EXAMINED. **Arabia:** Arabia orientalis, Trucial Oman coast, Jebel Ali, south of Dubei, *Field & Lazar* 14 V 1950 (GH); Süd-Arabien, Wadi Schigu bei Balhaf, *Schweinfurth 147*, fl. & fr., 27 III 1881 (US). **Iran:** Prov. Kerman, Bam to Faradj, limit. austral. deserti Lut, *Aellen & Esfandiari 3902* (MO, UC); same specimen, *Rechinger II-3902* (US). **Pakistan:** near Karachi, *S. ul Abedin 1394* (NY); Karachi University Campus, cult., *Asad Raza 99* (MO). **India:** Punjab, Ghogripur Jungle, Karnal Distr., *Drummond 24318, 24319, 24320, 24322* (UC); Flora Pentapotamica, Hansi in ditione Hissar, *Drummond 15139, 15140* (UC); Punjab, Gujranwala Distr., Rougah Drogan Desert, *Stewart 1426* (NY); India orientalis, *Wight 877* (GH); Hort. Bot. Calcuttensis (US 325480).

USES. According to Sarwar *et al.* (Pakistan Jour. Sci. Ind. Res. 10: 248–250. 1967, under *P. spicigera*), this tree grows up to 20 feet in the former Punjab and is evergreen, being the chief tree in localities where the rainfall is less than 30 inches a year. Its rather scanty, purplish-

brown heartwood is preferred to other kinds for firewood. It contains sugars, 5 flavonones, fatty acids, and tannins. It is not used commercially.

2. **Prosopis farcta** (Solander ex Russell) Macbride, Contr. Gray Herb. n.s. **59**: 17. 1919; Burkart, Darwiniana **4**: 62. 1940; *Prosopis farcta* (Banks & Solander) Eig, Jour. Bot. (Brit.) **75**: 189. 1937 ("*farcata*"). BASIONYM: *Mimosa farcta* Solander ex Russell, The Natural History of Aleppo, ed. 2. **2**: 266. 1794.

Mimosa stephaniana M. Bieb. Beschreibung der Länder zwischen den Flüssen Terek und Kur am Caspischen Meere. 120, 205. 1800.

Acacia stephaniana (*M. Bieb.*) Willdenow, Sp. Pl. **4**(2): 1088. 1806; M. Bieb. Fl. Taur. Cauc. **2**: 449. 1808.

Prosopis stephaniana (M. Bieb.) Kunth ex Sprengel, Syst. Veg. **2**: 326. 1825.

Lagonychium stephanianum (M. Bieb.) M. Bieb. Suppl. Fl. Taur. Cauc. **3**: 288. 1819; DC. Prodr. **2**: 448. 1825.

Lagonychium farctum (Solander ex Russell) E. G. Bobrov in Komarov *et al.*, Fl. USSR **11**: 13. 1945 (ed. Israel Program Sci. Transl., Jerusalem **11**: 13. 1971).

? *Prosopis aculeata* Koenig, Asiatic Researches **4**: *lám. X.* 18 . . . , according to Pritzel, Icon. Bot. Index, 1866.

ILLUSTRATION. Bobrov, *loc. cit.* 17. *fig. 1*, sub *Lagonychium.*

Prickly shrubs or subshrubs 30–80 cm. high; sometimes "shrub-trees" of 2–3 m. or more, subscandent, deep-rooted, and invading by root-suckers (or rhizomes?); branchlets with white-cinereous cortex; internodes with dispersed straight prickles 3–5 mm. long, the basal part of the petiole and peduncle often with one prickle, broad at base, dilated. Leaves recalling those of the *Acacia farnesiana* group, small, (2–)3–7-jugate, commonly 4–6-jugate, pubescent (glabrous in one variety); rachis plus petiole 1–3 cm. long, the pinnae 1–2.3 cm. long; leaflets in 10–15 pairs per pinna, dimidiate-lanceolate, auriculate, nearly enervate, pubescent (glabrous in one variety), 2–6.5 mm. long; stipules foliaceous, ovate-acute, larger than the leaflets, 3–6 mm. long, pubescent, very caducous. Racemes simple, axillary, glabrous, elongate, 4–12 cm. long, multiflorous, exceeding the leaves; peduncles solitary, lacking a primary bract, pubescent, often with a prickle at base; flowers pedicelled (but many aborting), green, creamy-greenish or yellowish-white, the buds acuminate; calyx 1 mm. long, puberulous; corolla 3.5–4 mm. long, glabrous outside and within, the petals linear, nearly free; stamens 4–5 mm. long, the anthers 0.8–1 mm., with an incurved apical gland; ovary entirely glabrous. Legume ca. 1.5–4.5 cm. long × 1.5–2.5 cm. thick, turgid, globose to cylindric, glabrous, subfalcate; placental suture somewhat prominent, the opposite one sulcate; exocarp shiny, smooth, orange-red, becoming black when ripe, thin, brittle; mesocarp spongy or farinaceous, apparently dry; endocarp thin, segmented, with transverse articles in two longitudinal rows; seeds also transverse, brown, ovoid-compressed, 7–8.5 mm.

long × 5–6 mm. broad × 2.5–3 mm. thick, with an open horse-shoe fissural line on the faces.

DISTRIBUTION. North Africa (Tunisia, Algeria (rare), Egypt) and southwestern Asia (Asia minor, Cyprus, Syria, Palestine, Iraq, Iran, Caucasia, Afghanistan, Pakistan, India: Punjab).

COMMON NAMES. Acatia; schamuth (Arabic); tofshandrnaq (Cau-casus orientalis), secundum M. Bieberstein "leporis unguem significante"; kharnub, shok, according to Blakelock, Kew Bull. 3: 419. 1948 (Iraq).

ECOLOGICAL AND ECONOMIC NOTES. Flowering takes place from June to August and the legumes mature from August to October.

Widely distributed but apparently rare at its western limits, e.g. in eastern Algeria (Quezel & Santa, Nouvelle Flore de l'Algérie 1: 556. *fig. 1634*. 1962, sub *Prosopis stephaniana*). While collecting in Cyprus, David Fairchild was impressed by the economic potential of the plant and referred to it as a range shrub for dry lands "good in spring for sheep and goats and cattle, a splendid bee plant, [which] roots very deeply" (June 25, 1930, in schedula). In the countries of the Near East it is abundant, but there it is sometimes considered a weed, especially in Transcaucasia, where Bobrov (*loc. cit.*) called it "a noxious weed, readily spreading due to the formation of root-suckers. Because of the spiny branches, it is little eaten by livestock and then only when young. The roots contain tannids and may be of interest as a tanning agent."

Eig, Feinbrun, and Zohary (in a note on the label of their collection no. *247* from the Mediterranean coast of Israel) are more appreciative. They refer to the species as "a most important plant, both in the Irano-Turanian countries and in the countries of its penetration in the Mediterranean region. Its main ecological requirements are deep alluvial soils, especially with shallow ground water. This seems to be the cause of its absence in the Mediterranean mountain districts of Palestine. But in the Irano-Turanian region, its main area, it is less sensitive to the edaphic conditions and there we found it also in the mountain districts. *P. stephaniana* is a leading plant in several associations of Palestine. . . . We met the most curious form of this species in the *Populetum euphraticae* of the Jordan Valley, where it is a bush-tree 2–3 m. high, or a liana, climbing sometimes as high as 8–10 m. on the *Populus euphratica* trees. Extremely common in fields of the maritime and interior plains."

The habit of *Prosopis farcta* as an invading shrub with root-suckers or rhizomes, brings it nearer to *P. strombulifera* (Lam.) Bentham than to any species of section ALGAROBIA in America, but *P. farcta* is not known as a weed, as it thrives in nontilled, saline soils under semiarid conditions.

Eshel and Waisel (Israel Jour. Bot. **14**: 50, 51. 1965) have studied the salt relations in the growth of this species of *Prosopis*.

The western border of its natural area seems to be Algeria and Tunisia (see A. Labbe, Bull. Soc. Sci. Nat. Tunisie **8**: 201. 1955 (sub *P. stephaniana*).

Neubauer (Ann. Naturh. Mus. Wien 60: 87. 1955, sub *P. stephaniana*) observed, in northern Afghanistan, that the species is an invader in wheat and cotton fields, frequent on clayey, dry soils; where it thrives best, the soils are considered of good quality.

SELECTED SPECIMENS EXAMINED. **Egypt:** Nil-Thal, Belbes, *Schweinfurth 43*, 1880 (R, US); Kharga, *N. El Hadidi*, 13 VIII 1967 (MO). **Cyprus:** Yerolakkos, *Larsen 851* (UC); Nicotia, *Kotschy 983* (GH); Epikho, near Kythraea, *Fairchild*, Armour Exped. *3572* (US); Limassol, *Mavromoustakis 7, 8, 9* (MO). **USSR.** TRANSCAUCASIA: Baku, *Prilipko*, 4 VI 1927, *Matveeva 805* (NY), *Svovitz 593* (US), steppe, *Heideman et al.*, 2 VIII 1929 (UC); Caucasus, C. Czermak, Muratinsk region, *Knorring & Emme 106* (US). TURKESTAN: Buchara, Hissar, *Bornmüller 932* (GH); Regio Transcaspica, Aschabad in steppis ad Mekrowa, *Sintenis 445*, Kisil Arwat, Karakala, *Sintenis 1932*, Plant. Turcomaniae, *Litwinow 122*, Atropatania, Balachany, *Petunnikov 3332* (GH, NY, US); Turkestania, *Korshinsky 1256* (GH), *1269* (US), *Regel* (SI 1047); Sallien et Mingatschour Georg. Cauc., *Hohenacker*, Unio Itiner. *1838* (MO). **Turkey:** Mersina stationary sand dunes, *Eig & Zohary*, 12 VIII 1931 (HUJ, UC); Cilicia, Plaine de Mersina, *Balansa 491* (GH, US). **Palestine:** east of Jordan, *Paine*, 1873 (US); Esdraelon Plain, *Zohary* (HUJ); near Tel Aviv, *Eig, Feinbrun, & Zohary 247* (GH, NY, US); Jericho versus Mare Mortum, *Ball 916* (GH); Palestina maritima, *F. Meyers 250* (GH); W. lower Galilee, Tivon, *Feinbrun* (HUJ 16398); Tel Aviv, cultivated ground, *Eig, Feinbrun, & Amdursky*, VII 1933 (Fl. Palaest. Exsicc. 247; HUJ). **Syria:** in planitie prope Aleppum, *E. Boissier*, VI 1846 (GH); Aleppo, *Sintenis 1447*, 26 VIII 1888 (GH); Damascus, *Dingler* (GH); Palmyra, *Field & Lazar 351* (GH). **Iran:** Prov. Kerman, *Bornmüller 3654* (GH, US); Iran, without further locality, *Rechinger II 6800* (UC, US); Persia, garden ad Rayy, *Field & Lazar 998*, Persia austro-orientalis, *Bornmüller 3655, 3656* (GH); Gurgan, in fields, *Koelz 16110* (US); Chesmagirin, Bakhtiari, *Koelz 15277* (US); Iran (?), in planit. Scheherisur, *Haussknecht* (UC); Persia, in desert. argilloso-salsis ad Cyrum, *Hohenacker* (CORD, MO, SI); Khuzestan, W of Behbahan, *Grant 15909* (MO); Kurdistania, Mardin Wüste gegen Khurs, *Sintenis 1039* (GH). **Afghanistan:** Baghlan, 3000 ft. elev., *Koelz 12176* (US); Helmund Valley, *Long 394* (US). **Iraq:** Abul al Kasib, Basrah Liwa, date orchard, *Barkley & Abbas al Ani 8905* (GH); Falluja, Bagdad Liwa, *Grant & Barkley 8560* (NY); Wadi Bakok, Mosul, *Grant & Barkley 8990* (GH); Kut Liwa, near Nuamaniya, Digila River, *J. Brahim M. 6191* (NY); Inter Chanikin et Baghdad, *Rechinger 2147*, Baghdad Liwa, *Abbas & Brahim 13* (MO). **Pakistan:** (?) N.W. Himalaya, Peshawar, N.W.F.P., Islamia College, *Stewart 9161* (NY).

Prosopis farcta var. **glabra** Burkart, var. nov.

A var. *farcta* differt foliis foliolisque omnino glabris, tota planta glabra.

TYPUS VARIETATIS: Iran. Persia austro-orientalis, Kerman, *Bornmüller 3654*, flowering, 18 V 1892 (holotype, US; isotype, SI 1044).

This variety is distinguished from *Prosopis farcta* var. *farcta*, by its entirely glabrous leaves, leaflets, and branches.

OBSERVATIONS. Other specimens of var. *glabra*: Transcaspia, *Sintenis 1932* (MO, US); USSR, Transcaucasia (?), *Kapa-Kaua 2840* (MO).

3. **Prosopis koelziana** Burkart, sp. **nov.**

Affinis *Prosopidis cinerariae*, arborea, aculeata, cortice cinereo; aculei sparsi 3–6 mm. longi; folia 2–3-juga (an semper ?), subglabra, pinnae 1.5–2 cm. longae, foliola 10–11-juga, rachides subpilosae; foliola 3–5 mm. longa × 1.1–1.5 mm. lata, lanceolata subdimidiata acuta subfalcata obscure 1–2-nervosa, margine exteriori ciliolato caeterum glabra. Spicae axillares solitariae 6 7 cm. longae; flores desunt. Legumen lineare, 4–6 cm. longum × 8 -10 mm. latum, ad basin cuneatum breviterque stipitatum, subtorulosum subrectum puniceum, stipite 0.8–1 cm. acumine 5 mm. longo; indehiscens subcoriaceum farctum; semina circiter 6–8 in pseudoloculis ovatis oblique transversis, subcompressa ovata fusca, 5–5.5 mm. longa.

TYPE SPECIMEN. **Iran**: Madenu, Kirman, in desert, *Koelz 14246*, December 26, 1939 (US 2194261, holotype).

This new species is intermediate between *Prosopis cineraria* (L.) Druce and *P. farcta* (Solander ex Russell) Macbride, the leaves being similar to those of the first species. It is easily distinguished from both of these species, however, by its peculiar fruits, which are stipitate and cuneate at base as in *P. cineraria*, but much shorter, thicker, and with transverse seeds, approaching by this character *P. farcta*. However, in *P. farcta*, the pods are much thicker, shorter and abruptly narrowed at base. It may be a natural hybridogen "stirps" originated by the cross *P. cineraria* × *P. farcta*. According to the collector, it is a tree up to 10 feet high, with crimson-colored fruits. The material is scarce, but the ripe legumes are very characteristic and different from those of any species known at present. Their red color seems to be a good character; the ripe fruit of *P. farcta* appears to be black and that of *P. cineraria* brown.

OBSERVATIONS. This species is named for the collector, Dr. Walter Norman Koelz of Michigan, U.S.A., a zoologist and botanist temporarily engaged in Asiatic research (see: American Men of Science, A Biographical Directory, ed. 11. Physical and Biological Sciences. 2861. J. Cattell Press, New York & London. 1965). The type may be a duplicate of a specimen at the University of Michigan, Ann Arbor, which I have not seen.

Sect. ANONYCHIUM

4. **Prosopis africana** (Guill., Perr., & Rich.) Taubert in Engler & Prantl, Nat. Pflanzenfam. 3(3): 119. 1891; Burkart, Darwiniana 4: 62. 1940; Brenan in Hubbard & Milne-Redhead, Fl. Trop. E. Africa, Leguminosae subfam. Mimosoideae, 36. 1959.

Coulteria ? africana Guill., Perr. & Rich., Florae Senegambiae Tentamen 1: 256. 1830.

Prosopis oblonga Bentham, Hooker's Jour. Bot. 4: 348. 1842; Bentham, "Revision of the Suborder Mimoseae," Trans. Linn. Soc. 30: 377. 1875; E. G. Baker, The Leguminosae of Tropical Africa 3: 805. 1930.
Prosopis lanceolata Bentham, Hooker's Jour. Bot. 4: 347. 1842.

ILLUSTRATIONS. Volkens, Notizbl. Bot. Gart. Berlin, App. 22: 10. 1909; Engler, Die Vegetation der Erde 9. Pflanzenwelt Afrikas 3(1): 394. *fig. 225*. 1915; Brenan in Fl. Trop. E. Africa, 35. *fig. 10*. 1959; Institut Français d'Afrique Noire, Icones Pl. Afr. 2: 30. Ifan-Dakar. 1953. G. Figueiredo & A. Sousa, Mém. Soc. Brot. Univ. Coimbra 1: 37. *tab. 23*. 1930 (sub *P. oblonga* Bentham).

Unarmed, tall trees, ca. 4–20 m. high; branches without axillary brachyblasts, the twigs and leaves somewhat pubescent, the branchlets and leaves dullish red when dry. Leaves drooping, 1–4-jugate, ample, the petiole 3–5 cm., the rachis 5–9 cm., the pinnae 6–15 cm. long; leaflets in 4–13 pairs, opposite, variable, ovate-lanceolate, 1.3–3.5 cm. long × 0.4–1.5 cm. broad, glabrous or finely pubescent, costate to slightly pinnatinerved, uniformly colored, reddish when dry, the midvein subcentral, the acroscopic half of the leaflet slightly larger. Racemes spiciform, ca. 5–9 cm. long, axillary, solitary or geminate, densely flowered; rachis pubescent; pedicels 0.5 mm. long, pubescent; flowers small, yellowish or greenish-white, perfumed; calyx 1 mm. long, pubescent; corolla 3.5 mm. long, the petals linear, free, glabrous on both sides; anthers with apically broadened and apiculate, incurved connective, pedicelled gland globose and incurved; pollen with costae on the pores; ovary and style pilose to villous. Legume indehiscent, straight to subfalcate, brown to blackish, shiny, subterete, 10–20 cm. long × 1.5–3.3 cm. in diameter; exocarp hard, 1–2 mm. thick; mesocarp spongy, massive, apparently dry; endocarp segments thin, longitudinal in one row; seeds many, dark, shiny, ovate-compressed, 8–10 mm. long × 4–9 mm. wide, with endosperm; fissural line large, submarginal; mature fruit sounding like rattlesnake tails when shaken.

AREA AND ECOLOGY. Tropical Africa, the whole savannah belt south of the Sahara and north of the great rain forest districts, especially in mesophytic woodland, from Guinea to the Sudan, Uganda, and Ethiopia.

USES. The bark is used as a medicine in case of fevers. The wood has a great variety of uses, including its use as a charcoal; in certain countries stands of *Prosopis africana* have been destroyed by exhaustive exploitation (see Adam, Echart, & Lescot, "Plant. Médic. Hausa de l'Ader (Rép. Niger)," Jour. Agr. Trop. Bot. Appl. 19(8–9): 331. 1972). Unlike the American *Algarobiae*, the fruits seem to be dry and inedible. The wood is hard and very resistant to putrefaction and insect attack. *Prosopis africana* is a tree of quick growth (Devillers & Schnell, Icon. Pl. Afr. 2: 29. 1953) and probably worthy of trials for reforestation programs.

MATERIAL EXAMINED. **West Tropical Africa:** without further locality, *Mann 1193* (GH, NY). **Nigeria:** northern part, *Yates 15* (K), *J. M. Dalziel s.n.* (MO).

Senegambia: *Heudelot*, photograph of type of *P. oblonga* Bentham (US). **Guiné-Bissau:** Estrada de Prabis, *Brigada Estac. Florestais Guiné no. 10* (R 76448); *Bor*, Espirito Santo Expl. Bot. *1* (MO). **Sierra Leone:** *Small 446* (MO). **Ghana:** Gold Coast, savannah forest tree, Epira, *Vigne 2042* (GH, MO, US); Yalinga, Haut Drebangui, *Le Testu 2703* (GH, NY, UC). **East Tropical Africa. Uganda:** Akka Ferry, Aswa River, Chua, *Eggeling E-1688* (MO, NY); Uganda, without further locality, *Lind 2414* (MO). **Ethiopia:** Nubaland, Tira, *Kotschy 381* (NY, isotype of *P.*(?) *lanceolata*).

Sect. STROMBOCARPA
Ser. Strombocarpae

5. **Prosopis strombulifera** (Lam.) Bentham, Hooker's Jour. Bot. **4**: 352. 1842; Bentham, Trans. Linn. Soc. London **30**: 380. 1875; Burkart, Darwiniana **4**: 71. 1940. BASIONYM: *Mimosa strumbulifera* Lamarck, Encycl. Méth. Bot. 1: 15. 1783 ("1789").

Acacia strumbulifera (Lam.) Willdenow, Sp. Pl. ed. 4. **4**(2): 1055. 1805; DC. Prodr. **2**: 455. 1825.
Spirolobium australe D'Orbigny, Sertum Patagonicum *tab. 13*. 1839.
Strombocarpa strombulifera (Lam.) A. Gray, Boston Jour. Nat. Hist. **5**: 243. 1845; Bot. United States Expl. Exped. **1**: 475. 1854; Hutchinson, Genera of Flowering Plants **1**: 287. 1964.

Spiny shrub 0.15–1.5(–3) m. high, with small foliage and long underground, spreading, horizontal runners (probably gemmiferous roots); branches flexuous, the spiny stipules straight, cinereous, very decurrent, 0.1–2 cm. long. Leaves 1-jugate, glaucous, puberulous or glabrescent; petiole 2–15 mm. long, the pinnae 1–3 cm. long; leaflets distant, alternate to opposite, 3–8 pairs per pinna, the distance between pairs 1 to 3 times their own width, in the upper leaves somewhat less; leaflets oblong, obtuse, enervate or slightly 1–3-nerved at base, 2–9 mm. long × 0.8–2 mm. broad. Peduncles axillary, solitary, 1.5–5 cm. long, elongating when the fruits ripen; globose heads ca. 1.5 cm. in diameter at anthesis; flowers yellow, the young filaments red; calyx and corolla striate, the former puberulous, 1.5–2.2 mm. long, the petals united the distance of their width, 3–4 mm. long, villous within; stamens and style exserted; ovary villous. Fruits lemon-yellow when ripe, puberulous when young, radiating (1–21 in number) from the receptacle as straight cylindrical bodies 1.8–5.2 cm. long × 0.6–1.0 cm. in diameter, formed by 8 to 17 dense, closed, regular coils (like corkscrews) each, 3–5 mm. thick; exocarp crustaceous; endocarp delicately segmented in longitudinal articles that are easy to open; mesocarp pulpy, tannic, reddish; seeds ovate, grayish green, 4.5–5.4 mm. long.

COMMON NAMES. Retortuño; mastuerzo; espinilla; algarrobilla; pata de loro; seca trapo; retortón (Chile).

DISTRIBUTION. Western Argentina; northern Chile. Also Peru, Huancavelica, Mayocc, according to C. Vargas (Rev. Fac. Ci. Univ. N. S. An-

tonio Abad, Cuzco, 2: 3–6. 1968), but the illustration given (*fig. 1*) and the specimens collected agree better with *P. reptans*.

One specimen seen from the United States, Imperial Co., California (see below) was introduced, but is reported as escaped (Munz, 1959, cited by D. Isely, Madroño 21: 296. 1972). Clos, in Gay, Fl. Chilena 2: 249. 1846, states that this screwbean was cultivated in gardens at Santiago, Chile, at that time, the fruits being used as a remedy for toothache.

MATERIAL EXAMINED. **United States.** CALIFORNIA: Imperial Co., Bard, SW corner of the old U.S. Dept. Agriculture Exp. Sta., *Osborn & Flock*, 3 VII 1963 (UC). **Chile:** Tarapaca, *R. A. Philippi*, 1888 (US); Atacama, Copiapó, *Werdermann 932* (MO, NY); Copiapó, *I. M. Johnston 4980* (US); Coquimbo, Ovalle, La Chimba, *Kausel 3300* (NY, SI); La Chimba, *Wagenknecht 168* (SI), *C. Jiles P. 497* (SI); Aconcagua, *Mexia 7850* (NY, US); Rancagua, in hortis cult., *Bertero*, Oct. 1828 (SGO). **Argentina.** SALTA: Cafayate, *Senn 4115*, *Humbert 21039*, *Killip 39542* (US); Cafayate, *Hueck 4* (SI); Cafayate a Sta. Bárbara, *Ruiz Leal 12200* (SI). TUCUMÁN: Tafí, *Venturi 4274* (LP, US); Valles Calchaquíes, *Castillón 9020* (LIL, SI). CÓRDOBA: Dept. Ischilín, S. José de las Salinas, *Hosseus 687* (CORD). LA RIOJA: Salinas Grandes, entre Baldes y Nabar, *Hieronymus & Niederlein 158* (CORD); Vinchina, *Covas 1270* (NY); *J. H. Hunziker 2036*); Villa Unión, *T. Meyer 4149* (UC, US); Villa Castelli, *T. Meyer 4066* (UC, US); General Lavalle, Los Palacios, *Palacios, Balegno & Cuezzo 1655* (MO). SAN JUAN: S. Juan a Calingasta, *Sayago 2458* (SI); Calingasta, Pachaco, *Rodrigo 3042* (LP, SI); Ullún, *Rodrigo 2825* (LP, SI); Valle del Zonda, *Bartlett 20511* (SI, US); S. Juan a Mendoza, Km. 24, *Nicora 4278* (GH, SI); Dept. Albardón, El Salado, *Volponi & Zardini 97* (LP, SI). MENDOZA: Sta. Rosa, Las Catitas, *Ruiz Leal 7976–220* (US); Travesía, Herb. *Miers 447* (US); La Paz, Paso de las Tropas, *Ruiz Leal 9932* (SI); Las Heras, Borbollón, *J. H. Hunziker 3155*, *Soriano 1107* (SI); Dept. San Martín a Sta. Rosa, *Ruiz Leal 9588*, Maipu, *Ruiz Leal 1648*, Las Heras, *Ruiz Leal 3550*, Las Catitas, *De la Barrera 2223* (SI); San Rafael, *Dawson & Pujals 1681* (BAB, SI); Rivadavia, *Catena*, Herb. *O. Boelcke 476* (SI); Dept. La Paz, Desaguadero a Bajada del Gato, *Ruiz Leal 8885, 8931* (SI); Luján, Dique Cipoletti, *Dawson & Pujals 1387* (BAB, SI); Mendoza, without further locality, *Rose & Russell 20974* (NY, US). SAN LUIS: Las Palmas, *Isern 8060* (MA, SI); El Morro, *F. Pastore 29*, Alto Pencoso, *Bruch & Carette 100* (SI); Dept. Pedernera, Cramer a Villa Reynolds, *Anderson 1499*, *B. S. Vuilleumier 1010* (GH, SI). NEUQUÉN: Cabo Alarcón, camino de Piedra del Aguila a Neuquén, *Nicora 4000* (SI). RÍO NEGRO: Cipoletti, *Rasp 82* (SI), *Scala 34* (NY); General Roca, *Soriano 1233* (SI), *Fischer 72* (MO, NY, US); Pichi Mahuida, *O'Donell 1589*, *Eyerdam, Beetle, & Grondona*, Univ. Calif. Exp. Andes, II *23473* (SI); Dept. Conesa, Conesa, *Eyerdam, Beetle, & Grondona*, Univ. Calif. Exp. Andes, II *23558* (MO, SI); Conesa, *T. Meyer 7083* (SI). LA PAMPA: Guatraché, *J. J. de Hernández ex Burkart 5956* (SI); General Acha a Lihuel Calel, Laguna La Asturiana, *Bacigalupo* (SI 20522). BUENOS AIRES: Partido Villarino, Pedro Luro, *Bartlett 19921* (SI, US). ARGENTINA, without further locality (Córdoba?), "Pampas," *Kuntze*, I 1892 (US).

USES. The fruit of *Prosopis strombulifera* is commonly collected and offered for sale in markets as a remedy. The Italian traveler and botanist C. Bertero found the plant grown in central Chile (Rancagua, *in hortis*)

in the year 1828 and noted that the legume was considered a remedy. Perhaps its curious shape lends itself to being used for imaginary cures. Hosseus states that the fruits are astringent and diuretic.

The roots contain a brown dye and may be used for tanning.

Prosopis strombulifera (Lam.) Bentham, var. **ruiziana** Burkart, var. nov.

A typo differt solummodo fructibus duplo maioribus crassioribusque, i.e., 6–7 cm. longis × 1.3–1.4 cm. diametro, spiris 12, 5–6 mm. crassis, ad medium subsulcatis; fructuum numero per capitulum 1 vel 2 (in var. *strombulifera*, 1–21).

This variety differs from the common typical variety in its large fruits, 6–7 cm. long × 1.3–1.4 cm. thick, with 12 coils 5–6 mm. thick; there are only 1 or 2 legumes formed on each flower-head.

Prosopis strombulifera var. *ruiziana* is dedicated to the collector, Professor Dr. h. c. Adrián Ruiz Leal, University of Cuyo, Mendoza, Argentina, who discovered it. *Prosopis strombulifera* var. *ruiziana* was growing with var. *strombulifera* and was selected intentionally because of the fruits, nearly twice the size of those of var. *strombulifera*, and the correlated small number of legumes per head, in contrast to var. *strombulifera*, in which these number from one to as many as 21 per head.

TYPE SPECIMEN. **Argentina.** MENDOZA: Dept. Junín, in aridis salsis inter Barrancas et Rodríguez Peña, *Adrián Ruiz Leal 3787*, with mature fruits, 25 II 1936 (holotype SI; isotype in Herb. Ruiz Leal, Univ. Cuyo).

This may be a natural tetraploid form.

6. **Prosopis reptans** Bentham, Hooker's Jour. Bot. **4**: 352. 1842; Bentham, Trans. Linn. Soc. London **30**: 381. 1875; Burkart, Darwiniana **4**: 74. *tab. V.* 1940.

Strombocarpa reptans (Bentham) A. Gray, United States Expl. Exped. Bot. **1**: 475. 1854.

Prosopis abbreviata Bentham var. *argentina* Grisebach, Pl. Lorentzianae in Abhandl. Ges. Wissensch. Goettingen **19**: 85. 1874.

Low, spiny desert shrub, with underground runners (gemmiferous roots or rhizomes?) by which it invades the soil. Very near *P. strombulifera* in all of its characters, but with different leaves; leaflets smaller, more pubescent and close to each other on the rachis of the pinna, even on the long shoots, so as to touch by their margins or become imbricated when in "sleeping" position. Heads axillary, globose; corolla striate. Fruits yellow, in close, dense, regular, numerous (up to 19) spirals, forming a cylindrical body ca. 5 cm. long × 7 mm. diameter, held in radiate position and not intermingling.

DISTRIBUTION. Central Argentina; apparently also in Peru.

COMMON NAMES. Mastuerzo; retortuño.

MATERIAL EXAMINED. **Peru:** Huancavelica, Mayocc, at 2100 m. elev., *Diers 942*, flowering, 11 XII 1960 (SI); Tayacaja, Mayocc, *Vargas 12856* (MO). **Argentina.** TUCUMÁN: Cruz Alta, Aráoz, *Schreiter 3977* (LIL, SI); Leales, Tres Pozos, *Descole & Schreiter* (LIL 68255; SI); Cruz Alta, *Venturi 7495* (US); Leales, *Villa Carenzo 3497*, *De la Sota 132* (LIL). SANTIAGO DEL ESTERO: Brea Pozo a Río Huayco Hondo, *Bartlett 19748* (NY, SI, US); Colonia Dora a Angá, *Ragonese & Castiglioni 6680* (BAB, SI); Route 9, just south of Loreto, *B. S. Vuilleumier 1035* (GH, SI); Santiago del Estero, without further locality, *Arga-ñarás 135* (SI). CÓRDOBA: Totoralejos, borde de las Salinas, *Burkart 12913* (LIL, SI); Totoralejos, *O. Kuntze*, Nov. 1892; Cañada del Gobernador, *Isern 8030*, flowering, 13 II 1863 (MA, SI); Salinas Grandes, Km. 907, *Soriano 771*, *760* (SI); Cruz del Eje, *O'Donell 4530*, *T. Meyer 12837* (LIL); Dept. Rio Seco, Saladillo, *Sayago 2215*, Dept. Ischilín, Villa de Quilino, *Sayago 2094*, Dept. Tulumba, Totoralejos, *Sayago 2046* (SI); Salinas Grandes, *Lorentz & Hieronymus*, fruct., 10 XI 1872 (NY); Córdoba, without further locality, *Kuntze*, Dec. 1891 (NY). PROV. SANTA FE: Logroño, FCE, Estancia Las Norias, Dept., 9 de Julio, *Krapovickas 808*, Vera FCSF, *Burkart 5935* (SI).

OBSERVATIONS. This is the first mention of *Prosopis reptans* for Peru. It bridges the gap between the areas of var. *reptans* and var. *cinerascens* (see below).

Prosopis reptans Bentham var. **cinerascens** (A. Gray) Burkart, Darwiniana **4**: 75. 1940; Benson, Am. Jour. Bot. **30**: 238. 1943. BASIONYM: *Strombocarpa cinerascens* A. Gray, Pl. Wrightianae **1**: 61. 1852.

Prosopis cinerascens (A. Gray) Bentham, Trans. Linn. Soc. London **30**: 381. 1875; Benson, Am. Jour. Bot. **28**: 754. 1941; Isely, Madroño **21**: 289. 1972.

Spiny shrub 1–4 dm. tall, distinguished by more pubescence than in var. *reptans*; leaflets slightly larger (4 mm. long and pubescent or glabrous; calyx and corolla striate, as in related species, the calyx 2–2.5 mm. long, the corolla 4 mm. long; anthers 1.5 mm. long. Legume cylindrical, yellow, in 9 to 12 close, regular coils.

DISTRIBUTION. U.S.A.: Texas; adjoining Mexico (Isely, *loc. cit.*). Grows on saline soils.

COMMON NAMES. Screwbean; tornillo.

MATERIAL EXAMINED. **U.S.A.** TEXAS: Willacy Co., Port Mansfield, sand dunes at bay, *Creighton 131* (COLO); Brooks Co., *Gould, Reeves, & Morrow 6583* (UC); Point Isabel Road, *Rose & Russell 24258* (US); Green Island, *Tharp 1238*, Carrizo Springs, Dimmit Co., *E. J. Palmer 33766*, Laredo, *Orcutt 5775*, Brownsville, *Fisher 41121*, *Cory 51422*, *Schiller 938*, Cameron Co., *Traverse 1088* (MO, US); Webb Co., *Lundell 13804* (US); Lower Rio Grande, *A. Schott*, in 1853 (US); Webb Co., Aquilares, *Tharp et al. 51–1688* (LIL); Brownsville, clay dune, *Small & Wherry 11843* (LIL); Cameron Co., along coast, *Tharp & Gimbrede 52–519* (MEXU); Webb Co., *Lundell 13804* (TEX). **Mexico.** TAMAULIPAS: sudeste de Matamoros, *Medrano 663* (MEXU); Santa Teresa Laguna Madre, *Medrano 47* (ENCB).

FIGURE 2. **Prosopis.** Flowering and fruiting branchlets, × ⅝, of *P. abbreviata* (*Tinto 2018*), from La Laja, San Juan, Argentina.

OBSERVATIONS. Recent phytochemical analyses by N. J. Carman (1973) strongly support the specific identity of *Prosopis reptans* var. *reptans* and var. *cinerascens*. As could be expected from the morphological similarity, no differences from *Prosopis strombulifera* could be detected. Perhaps all three taxa are only one natural species with some variations. Even the recognition of the Texan plant as a variety is problematic.

Variation occurs in the Texan material of var. *cinerascens*. Tharp and Gimbrede's collection no. *52–519* bears glabrous leaflets and puberulous legumes.

7. **Prosopis abbreviata** Bentham, Hooker's Jour. Bot. 4: 352. 1842; Burkart, Darwiniana 4: 70. 1940; *Ibid.* 9: 77. 1949.

Strombocarpa abbreviata (Bentham) Hutchinson, Genera of Flowering Plants 1: 287. 1964.

Small tree, ca. 2–3 m. high; trunk short, to 10 cm. in diameter; branches armed with the spiny stipules characteristic of the section, up to 3.5 cm. long. Leaves unijugate, short-petioled, glabrous; leaflets minute, approximate, in 5–16, mostly 8–15 pairs per pinna. Flower heads ovoid-elliptic, the rachis 1 cm. long; peduncles axillary, 1.5–3 cm. long; calyx 2 mm., the petals 4 mm. long; ovary villous. Legumes in 2–7½ irregular, closed, dense spirals, coiled, 2–4 cm. long × 1–1.5 cm. in diameter, brownish, puberulous; endocarp segmented; seeds 4.5 × 3 mm. long and broad.

DISTRIBUTION. Endemic in west-central Argentina (in the provinces of Catamarca, Córdoba, Santiago del Estero, San Juan, and San Luis). A rather rare species, perhaps because of early exploitation. Used for firewood.

COMMON NAME. Algarrobillo espinoso.

MATERIAL EXAMINED. **Argentina.** CATAMARCA: Dept. Belén, Huiliche (La Ciénaga), *Schreiter* (LIL 68581; SI); El Carrizal, *Devoto & Rial Alberti*, Herb. Dir. Forestal *1686* (SI); Dept. Belén, La Ciénaga, *Sayago 2259 bis*, fl. & fruct., I 1956 (SI). CÓRDOBA: Salinas Grandes, Km. 907, *Soriano 793* (SI). SAN JUAN: La Laja, north of S. Juan, *J. C. Tinto*, Herb. Dir. Forestal *2018* (SI). SAN LUIS: Dept. Capital, Alto Pencoso, *Bruch & Carette 100* (LP, SI); Laguna Seca, *Bruch & Carette 211* (LP, SI).

OBSERVATIONS. *Prosopis abbreviata* is a well-marked species, with no problems of delimitation. *Prosopis torquata* is similar in its tree habit, but it has different fruits, with a few open coils. *Prosopis strombulifera* is shrubby with underground runners; its fruits have more numerous, regular coils and yellow exocarp. *Prosopis burkartii* has affinity with *P. abbreviata*, but is of a bushy, creeping habit, with longer spikes, larger leaflets and flowers, and more irregular, shorter legumes.

8. **Prosopis torquata** (Cavanilles ex Lagasca) DC. Prodr. 2: 448. 1825; Burkart, Darwiniana 4: 66. *illustr.* 1940.

Acacia torquata Cavanilles ex Lagasca, Elench. Pl. Hort. Matrit. 16. 1816; Lagasca, Gen. Sp. Pl. 16. 1816.

Prosopis adesmioides Grisebach, Pl. Lorentzianae in Abhandl. Ges. Wissensch. Goettingen 19: 84. 1874; cf. Burkart, *loc. cit.*

Strombocarpa torquata (Cavanilles ex Lagasca) Hutchinson, Genera of Flowering Plants 1: 287. 1964.

Erect or spreading shrub or small tree 1–5 m. high, spiny, small-leaved; stipules spiny, as in the related species, more robust on vigorous shoots, 0.1–5.5 cm. long. Leaves 1-jugate; petiole 1–4 mm. long; leaflets 14–30 pairs per pinna, approximate to imbricate, small, oblong, obtuse to sub-

acute, 1-nerved, glabrous or mostly pubescent, 2–4 mm. long × 0.6–0.8 mm. broad; pinnae 0.5–3.5 cm. long. Spikes axillary, ovoid to cylindric, 3–8 cm. long (including peduncle of ca. 1 cm.); flowers about 40–55 per inflorescence, bright yellow, sessile, glabrous outside; calyx 1.5 mm. long; petals 3–4 mm. long, united to their middle; stamens twice as long; ovary villous, the style 4 mm. long. Fruit puberulent in 1–3 irregular spirals, these rather open; articles compressed-globose, with isthmi 2–5 mm. broad, excentric, each one 5–8 mm. long and broad; mesocarp pulpy; endocarp segments hard, closed, approximately 6 × 6 × 4 mm., disclike, ca. 8–13 per legume.

DISTRIBUTION. Argentina, northwestern provinces, apparently endemic. Common and important in the semidesert Monte-vegetation, from Salta southward to San Luis and Mendoza.

COMMON NAMES. Tintitaco, quenti; schinqui, tusca, lata.

MATERIAL EXAMINED. **Argentina.** SALTA: Cafayate a Sta. Bárbara, *Ruiz Leal 12198* (SI); Cafayate, *Krapovickas & Cristóbal 20679* (SI); S. Carlos, Angastaco, Ruta 40, *Krapovickas & Cristóbal 20639* (SI); Coronel Moldes, *Dawson & Calastremé 2012* (BAB, SI), *Bartlett 19667* (SI, US); Guachipas, *Peirano* (LIL 71730); Payogasta, *Ruiz Leal 21292* (SI); Rosario de la Frontera, *Schulz 6554* (SI); Alemania a Cafayate, *Schulz 6640* (SI). TUCUMÁN: Dept. Tafí, Amaicha, 2120 m. elev., *Krapovickas & Cristóbal 20546* (SI); Dept. Trancas, Vipos, *Lillo 7246*, *Schreiter 4596* (LIL, SI); Julipao (Cumbres, Calchaquíes, at 1900 m. elev.), *Morello 1248* (SI); Las Arcas a Tiapunco, *Schreiter 4739*, Cruz Alta, Tacanas, *Schreiter 4605* (SI). CATAMARCA: Belén, El Pozo, *Sayago 1584*, Cerro de la Banda, *Sayago 1478* (SI); Capital, Las Rejas, *Ulibarri 461* (SI); Andalgalá, *Parodi 14249* (SI); Campo Las Heras, *F. E. Devoto*, Herb. Forestal *1678* (SI); Campo de Belén, *Sayago 2011* (CORD, SI); Los Nacimientos, *Falcone & Castellanos*, Herb. Forestal *3554* (SI); La Puerta y Yacutula, *Sayago 640* (SI); Andalgalá, *Solbrig 4216* (GH, SI), *Joergensen 969* (MO). LA RIOJA: Gral. San Martín, Estancia Copahue de Mangino, *Anderson 1526* (SI); Chilecito, Cerro Bola, *Dawson 3436* (LP, SI); Chilecito, *T. Meyer 3511* (UC), *4101* (GH); Guandacol, *T. Meyer 4995* (US); Route 38, 38 km. south of La Rioja, *B. S. Vuilleumier 1019* (GH, SI); Route 9, 46 km. north of Bazán, *B. S. Vuilleumier 1021* (GH, SI). SAN JUAN: Jáchal, Cuesta de Huaco, *Ruiz Leal & Roig 18851* (SI), *Cabrera et al. 24556* (LP, SI); Jáchal, La Ciénaga, *Cabrera et al. 24542* (LP, SI); Valle Fértil, *Fabris & Zuloaga 8327* (LP, SI), *Piccinini & Leguizamón 1773* (SI); Caucete, camino a Vallecito, *Rodrigo 2876* (SI); S. Agustín del Valle Fértil, *Bartlett 19556* (SI, US); Pismanta, *Ruiz Leal & Roig 18979* (SI). SANTIAGO DEL ESTERO: Ojo de Agua, *Sayago 1379* (SI); Dept. Copo, Los Tigres, *Roig 8* (SI); Espada, *Argañarás 363* (SI); El Palomar a Pampa Pozo, *Schreiter 6720* (LIL, SI); Dept. Ojo de Agua, Navarro, *Sayago 2807b* (SI); Giménez, Gramilla, *Venturi 9749* (GH, MO). CÓRDOBA: Córdoba a La Calera, *Hieronymus 125* (CORD, US); San Javier, Loma Bola, *J. H. Humziker 8288* (SI); Capilla del Monte a Cruz del Eje, *Burkart 20408* (SI); Cerritos de Malagueño, *A. T. Humziker 7820* (CORD, SI); Dept. Tulumba, S. Pedro a Pozo del Algarrobo, *Sayago 1886* (SI); Sierras del Oeste, *Báez 27* (SI); Sta. María, Los Chinos, *Sayago 1422*, Río Seco, sierra, *Sayago 301* (SI). SAN LUIS: S. Luis de la Punta, *Isern 8062*, 10 III 1863 (MA, SI); La Calera, *Burkart 10716*, Alto Pencoso, *Ruiz Leal 9601*, *9605* (SI); De-

FIGURE 3. **Prosopis.** Flowering and fruiting branchlets, × 5/8, of *P. torquata* (*Cabrera 24556*). from Jachal, San Juan, Argentina.

saguadero a Jarilla, *Ruiz Leal 9092, 9442, 9934* (SI); Bajo de Velis, *Kurtz 8491* (R). MENDOZA: Dept. La Paz, Paso de las Tropas, *Ruiz Leal 9067* (SI).

USES. Wood for fuel.

9. **Prosopis pubescens** Bentham, London Jour. Bot. **5**: 82. 1846; Bentham, Trans. Linn. Soc. **30**: 380. 1875; Jepson, Fl. Calif. **2**: 240. 1936; Burkart, Darwiniana **4**: 69. 1940; Benson, Am. Jour. Bot. **28**: 753. 1941; Shreve & Wiggins, Fl. Sonoran Desert **1**: 603. 1964; Isely, Madroño **21**: 294. 1972; Standley, Contr. U. S. Nat. Herb. **23**: 350. 1922.

Strombocarpa pubescens (Bentham) A. Gray, Pl. Wrightianae **1**: 60. 1852; cf. Britton & Rose, N. Am. Fl. **23**(3): 183. 1928, in synon.

ILLUSTRATIONS. Sargent, Sylva N. America **3**: 107. *tab. 138*. 1890 (ed. 1947); Jour. Torrey Bot. Club Expl. California, in Rep. Expl. Surv., Railroad fr. Miss. R. to Pacific Ocean 5, **7**: 360. *pl. 4*. 1853.

Tall shrub or tree 2–10 m. high, much branched; trunk short, to 30–40 cm. in diameter; stipules spiny, straight, cinereous, decurrent, 0.2–2 cm. long. Leaves 1-jugate, short-petioled; leaflets elliptic-oblong, in 5–9 pairs per pinna, pubescent, not overlapping, slightly 1–3-nerved at base, subacute, 4–12 mm. long × 2–4 mm. broad. Spikes axillary, simple, elongate, 5–8 cm. long (including the peduncle of 1–1.5 cm.); florets pubescent, sessile, yellow; calyx 0.7–1.2 mm.; corolla 2–3 mm. long, gamopetalous, thin, the petals 1-costate, finely pubescent outside and on the inner apex; stamens 4–5 mm. long, the anthers 0.5–0.8 mm. long; ovary white-villous, the style glabrous; young fruit 4–5 mm. long, densely white-villous and already 2 to 3 times coiled. Fruits very similar to those of *P. strombulifera* and *P. reptans*, divergent on the rachis, never intermingling, puberulous or glabrescent, with 8–24 dense, closely set spirals, forming on the whole a cylindrical, yellow body 2.5–5.5 cm. long × 5–6 mm. in diameter; seeds reniform-ovoid, 3–3.5 mm. long; endocarp thin.

COMMON NAMES. Screwbean; tornillo.

DISTRIBUTION. Southwestern North America; Mexico (Baja California to Chihuahua); U.S.A. (California to Utah, Arizona, New Mexico, Nevada, Texas); bottomlands along streams and waterholes in desert climate; naturalized in South Africa.

MATERIAL EXAMINED. **U.S.A.** CALIFORNIA: San Bernardino Mts., *Parish 2982* (US); Colorado Desert, Riverside, lower Sonoran Zone, *C. B. Wolf*, Rancho Sta. Ana Bot. Gard. *4348* (COLO); Indio, *Thackery 377* (COLO); Imperial Valley, *J. B. Marks*, IV 1948 (LIL); California, *Brandegee*, V 1912 (UC 185747); N. lower Calif., *C. R. Orcutt*, 27 VII 1885, S. Diego Co., *Abrams 3999* (NY); Riverside Co., Palo Verde Valley, *Carter 1430* (MO, NY, US); Riverside Co., W. Colorado Desert, *M. D. Clary*, V 1931 (SI); Little S. Bernardino, *Munz & Johnston 11231* (SI). NEVADA: Clark Co., Charleston Mts., *Clokey 8397* (LIL, MO, NY, US); Las Vegas on Highway 91, *Raeder 171* (COLO). UTAH: Washington Co., St. George, *Eggleston 14789, 14793* (NY, US), *M. E. Jones 6089* (US). ARIZONA: Sacatón, *Harrison 163, Harrison & Kearney 2311* (US); Tucson, *Thomber 451* (US); Arizona, without further locality, *Pringle 1370* (BA, GOET). NEW MEXICO: Black Range, Animas Creek, Sierra Co., *Metcalfe 1116* (COLO, LIL, MO); Dona Ana Co., El Paso, *Lee, Berkman, & Tharp 46310* (UC); Dona

Ana Co., Mesilla Valley, *Wooton & Standley 3173* (COLO, NY, US), *Wooton 18* (MO, US); Jornada del Muerto, *G. Engelmann*, 29 VII 1846 (MO); New Mexico, without further locality, *E. O. Wooton*, 26 VI 1902 (COLO). TEXAS: Presidio Co., Sierra Tierra Vieja, *Hinckley 1897* (NY); Porvenir, *York 48245* (TEX); near Rio Grande, *Steiger 457* (NY); Presidio Co., along Rio Grande, *Cutler 1917* (MO, SI); Texas Co., *Turner 3654* (TEX); El Paso, *E. J. Palmer 31090* (MO). **Mexico:** Baja California, Alaska to Mexicali, *Wiggins & Gillespie 4178, 4179* (GH, MEXU, NY); Baja California, Mexicali, *Inst. Biol. Herb. 3454* (MEXU); Chihuahua, *C. G. Pringle*, 12 VIII 1887 (MEXU); Palm Valley, *C. R. Orcutt*, June-July 1883 (MO). **South Africa:** Carnarvon District, forming thickets along river at Van Wyk Vlei, *Acocks 1788*, flowering. II 1937 (NY).

OBSERVATIONS. A well-characterized species, without problems of delimitation. It has been called *Prosopis odorata* or *Strombocarpa odorata*, but these names are to be rejected (see Benson, 1941, and list of excluded names at end of this paper).

On one raceme normally only a few legumes develop, but in Cutler's specimen no. *1917*, from Presidio County, Texas (MO), as many as 35 unripe legumes are seen on the same peduncle.

USES. *Prosopis pubescens* is used as fuel; the legumes are important as food and forage for cattle.

10. **Prosopis palmeri** S. Watson, Proc. Am. Acad. Arts Sci. **24**: 48. 1889; Standley, Trees and Shrubs of Mexico, Contr. U. S. Natl. Herb. **23**(2): 351. 1922; Burkart, Darwiniana **4**: 62. 1940.

Sopropis palmeri (S. Watson) Britton & Rose, N. Am. Fl. **23**(3): 183. 1928; Hutchinson, Genera of Flowering Plants **1**: 290. 1964.

Shrub or tree 1.2–6(–7.5) m. high, much branched, spreading symmetrically, flat topped; trunk to 1–3 m. long, reaching 45 cm. in diameter; bark gray or dark purple, splitting off in long strips; branchlets spiny, finely pubescent or subglabrous; the spiny stipules as usual straight, paired, cinereous, 0.5–3.5 cm. long, caducous with age; wood very hard, dark purple; brachyblasts congested, perennial, blackish, elongating to 1–2 cm., capable of a reversion to macroblasts by apical growth. Leaves 1-jugate; petiole short, to 5 mm. long, the pinnae 2–3 cm. long; leaflets 3–10 pairs, glabrous, elliptic-oblong, obtuse or mucronate, tending to obovate, enervate or with 1 to 2 main nerves scarcely visible, 4–8 mm. long × 2–3 mm. broad. Spikes axillary, slender, 3.5–6 cm. long (the nude peduncle ca. 1.5 cm. long); flowers bright- or lemon-yellow, fragrant, sessile, tubular, puberulous; calyx 1.3–2.3 mm. long; corolla 5-toothed, angled, 4.5–6 mm. long, the petals connate for much of their length, pilose or subglabrous inside at their tips; stamens 10–12 mm. long, yellow, the anthers 0.8–1.5 mm. long; apical gland globose; ovary white-villous, the style pilose to glabrous. Legume straight to falcate, indehiscent, puberulous, almost terete to compressed, 4–9 cm. long × 0.8–1 cm. broad, reddish-brown, with delicate oblique striae forming a V, sessile, cuneate at

base, obtuse and mucronate at tip, the placental margin convex (legume recurved); exocarp thin, brittle, nearly membranous, subtended by a layer of longitudinal close-set fibers; mesocarp thin, brittle, tannic-reddish; endocarp tiny, membranous, segmented in one row, but opening easily at maturity, the segments rectangular; seeds numerous, oblique, oblong, brown, 6–7 mm. long; fissural line broadly open at base.

DISTRIBUTION. Mexico (Baja California); a narrow endemic, but locally abundant, as shown by the beautiful collections and remarks of H. S. Gentry and Miss Annetta Carter; grows mainly on dry riverbeds.

USES. Browsed by cattle and much used for fuel (Gentry).

COMMON NAMES. Palo de hierro; palo fierro.

MATERIAL EXAMINED. **Mexico:** Baja California, Muleje, *E. Palmer 2*, June 1887 (GH, type; NY); bank of Arroyo de la Presa, *Wiggins 15496* (GH, TEX); Médano a Venancio, *Wiggins 5545* (GH, NY, UC); Arroyo Hondo, Sierra de la Giganta, *Gentry 4164, 4165* (GH, MO); Magdalena Plain, Sauce, *Gentry 4189* (GH, UC); Sierra de la Giganta, *Carter 4935, 4275* (MO, NY, TEX), *4139* (LIL, UC), *4816, 5280* (MEXU, UC); Baja California, *Nelson & Goldman 7259, 7310* (NY); near Comondú, *Wiggins 5486* (NY, UC), *Carter 2477* (UC); 9.6 km. NE of Rosarito, *Carter 2944* (MEXU, UC); Concepción Bay, 24 miles S of Muleje, *Wiggins 11420* (GH, UC); Juncal y Purísima, *Brandegee s.n.*, 12 I 1890, 13 II 1889 (GH, UC); San Javier a Loreto, cerca de Comondú, *Chambers 964* (UC); 5 miles N of Comondú, *Hammerly 423* (GH).

OBSERVATIONS. This species has not been correctly interpreted up to now. The original author considered it, erroneously, as a member of sect. ALGAROBIA. He failed to recognize that the petals are, at least often, hairy inside their tips. Later, Britton and Rose (1928, p. 182) treated it as a new genus (*Sopropis*). To increase the confusion, I regret to state that in my former paper on *Prosopis* (1940, p. 62), misled by descriptions citing the petals as glabrous, I tentatively treated the species as approaching *P. africana* in sect. ANONYCHIUM, with which it has no affinity at all (as already shown by P. Guinet as a result of his pollen studies, *Les Mimosacées, Etud. Palynol. Fondament.*, Thèse Univ. Toulouse, p. 53. 1969). After a thorough comparison of the excellent material at the Berkeley, Harvard, St. Louis, and New York herbaria, it is clear to me that *P. palmeri* is a true STROMBOCARPA. While it is a very well-marked species within this section (the only one without fruits which coil), it nevertheless lacks qualifications to form a special group or genus because of its gamopetaly and sessile flowers, which also occur in several related species. Furthermore, the supposed absence of hairs inside the petal tips does not appear to be true, so there is no really sharp distinction from the ordinary condition. The key to the species presented by C. M. Rowell (in J. L. Schuster, Literature on the Mesquite (*Prosopis* L.) of N. America, An annotated bibliography. Texas Tech. Univ. 5. 1969) must therefore be emended.

11. **Prosopis burkartii** Muñoz; C. Muñoz Pizarro, Bol. Mus. Nac. Hist. Nat. Chile **32**: 363–370. *illustr.* 1973 ("1971").

Large, densely and intricately branched, creeping shrub 0.5–1.5 m. high; spiny stipules cinereous, 0.5–3 cm. long, decurrent as costae on the internodes. Leaves glabrous, unijugate; petiole short, 3–5 mm., the pinnae 2.5–3.5 cm. long; leaflets 7–12 pairs, elliptic-oblong, obtuse to subacute, glabrous or ciliolate, 4–7 mm. long × 1–2 mm. broad. Peduncles solitary, axillary, 2–3 cm. long, flower-spike short-cylindric, to 3 cm. long × 1.5 cm. in diameter. Flowers sessile; calyx puberulous, 3 mm. long; corolla 4–5 mm. long, the petals acute, glabrous outside, villous at the inner apex; stamens 5 mm. long, the anthers 1.5–1.8 mm. long; ovary white-villous, the styles glabrous (protruding in bud). Legumes puberulous, submoniliform in 1 to 3 spirals (placenta on the concave border), brown, mostly many legumes of a spike intermingled, forming a globose mass; endocarp segments and seeds longitudinal, the seeds 5.2 mm. long × 4 mm. broad.

DISTRIBUTION. Northern Chile, Prov. Tarapacá, Pampa del Tamarugal. This species is known only from the type locality, but Professor Otto Zoellner has written to me that he thinks he found more stands in the Camarones Valley, Tarapacá, unfortunately lacking flowers and fruits.

MATERIAL EXAMINED. **Chile:** Tarapacá, El Gobierno, La Guaica, *C. Muñoz Pizarro 7370* (SGO, SI).

OBSERVATIONS. The original description is contradictory concerning the position of the endocarp segments. These are not transverse, but rather longitudinal, as I have observed in the type material. Therefore, the species must find its place in ser. Strombocarpae. By its morphology and distribution, it may have originated from hybridization of *Prosopis tamarugo* × *P. strombulifera*, both of which occur in its area. The fertility of the material discovered by Professor Muñoz indicates a stabilized biotype.

Ser. Cavenicarpae (Burkart) Burkart

12. **Prosopis ferox** Grisebach, Symbolae ad floram Argentinam in Abh. Kön. Ges. Wiss. Göttingen **24**: 118. 1879; Burkart, Darwiniana **4**: 76. 1940.

Shrub or tree 2–5 m. high (with age up to 7 m. high), with a short trunk up to 1 m. in diameter; branches, leaves, and flowers of the general *Strombocarpa* type; stipular spines minute on brachyblasts, on macroblasts 1.5–5 cm. long, straight, cinereous, divergent, fused at base and decurrent on the branchlet. Leaves 1-jugate; petiole 1–3 mm. long, the pinnae 1–4 cm. long; leaflets 9–18 pairs per pinna, linear-oblong, mucronate, 3.5–8 mm. long × 1–1.5 mm. broad, glabrous or ciliolate. Spikes pedunculate, 2–6 cm. long; calyx 1–2 mm. long, glabrous; corolla ga-

mopetalous, 5–6 mm. long, glabrous outside; ovary villous. Legume straw-yellow when ripe, resembling *P. farcta* because of its thickness, cylindric, with prominent placental suture, straight or slightly falcate-incurved, not laterally coiled, 2.5–7 cm. long × 1–1.8 cm. in diameter, sessile, globose at base, obtuse and mucronate at apex; exocarp rigid, smooth, 1 mm. thick; mesocarp spongy, tannic(?), bitter; endocarp segments transverse in 2 irregular rows; seeds compressed, ovate, 4.5–6 mm. long.

DISTRIBUTION. Limited to southern Bolivia and the extreme northwest of Argentina in the Puna region of Jujuy and Salta provinces. Typical tree of the semidesert vegetation rich in cacti, in the Quebrada de Humahuaca; often the only tree there, growing at rather high elevations (2400 to 3700 m.). A historical tree, known to be nearly 200 years old, at Tilcara, Jujuy, measures ca. 7 m. tall, with a trunk 1 m. in diameter (*T. Meyer 22650* (SI)).

COMMON NAMES. Quiscataco; churqui; churqui jujeño.

MATERIAL EXAMINED. **Bolivia:** Prov. Nor-Chichas, Dept. Potosí, Quechisla, *Cárdenas 39* (GH). **Argentina.** JUJUY: Humahuaca, Puna, *Hieronymus & Lorentz 786*, III 1873 (phototype, Field Mus. 1461, GH, SI; specimens, CORD, GOET, NY); La Quiaca, *Pflanz 933* (M); Humahuaca, *Krapovickas 1521* (SI); Camino Iturbe a Humahuaca, *Soriano 689* (SI); Ruta 9, Uquía, *Okada 2995* (SI); Humahuaca, *Cabrera & Kiesling 20255* (LP, SI); Dept. Yaví, Yaví Chico, *Bolsi & Werner 5* (LIL, SI), *T. Meyer s.n.* (LIL 31466); Dept. Sta. Catalina, El Angosto, *Cabrera, Crisci & Kiesling 19881*, at 3700 m. elev. (LP, SI); Quebrada de Humahuaca, *Ruthsatz, 22* VIII 1971 (ripe fruits, SI 26540); Tilcara, *T. Meyer 22650* (LIL, SI). SALTA: Dept. Poma, Campo de la Paciencia cerca de Cerrillos, *Cabrera 8306* (LP, SI).

USES. Fuel, shade; fruits for food. In spite of its systematic affinity with *Prosopis tamarugo* (from Chile), *P. ferox* is probably not as valuable for desert reforestation purposes, since it is smaller, more spiny, and probably of slower growth.

13. **Prosopis tamarugo** F. Philippi, Verh. Deutsch. Wiss. Ver. Santiago, Chile 1: 159. 1886 (Index Kewensis Suppl. 9); Burkart, Darwiniana 4: 80. *fig. 4, tab. 7.* 1940; Maldonado, Rev. Chilena Hist. Nat. 22: 65–71. 1918; R. A. Philippi, Anal. Mus. Nac. Chile, 21. 1891.

Tree when old up to 18 m. high, very similar to *P. ferox*; stipules spiny, smaller, 0.5–3.8 cm. long; leaves unijugate, similar to those of *P. ferox*, pinnae 3–4 cm. long or less, with 10 to 15 pairs of leaflets, these linear, obtuse or subacute, 4–8 mm. long, more distant. Spikes axillary, 3.5–6.5 cm. long; flowers yellow, sessile, glabrous outside; calyx 1.5 mm.; corolla 4–5 mm. long, the petals united, the tips villous within; ovary villous. Legumes straw-yellow or clear brown, cylindric-subtorulose, turgid, of the same structure as in *P. ferox*, but more strongly incurved.

falcate to ring-shaped, smaller, 2 -3.5 cm. in diameter and thinner, 7–10 mm. thick, the sutures impressed; seeds smaller, ovate, 3–4.3 mm. long, brown.

COMMON NAME. Tamarugo.

DISTRIBUTION. Chile, only in the northern, desert provinces, especially in Tarapacá, where, on arid mesetas, it is the only tree; the region bears its name, "Pampa del Tamarugal." Its area of distribution covers the central strip of Tarapacá, south of Arica and Antofagasta and north of Chuquicamata, a surface of roughly 15,000 km.^{2} The natural stands are very scattered or devastated, however, since this is the only firewood over long desert expanses.

MATERIAL EXAMINED. **Chile:** Tarapacá, Pampa de Tamarugal, cerca de La Guaica, entre Pica y Pozo Almonte, *Hans Niemeyer*, X 1962, Herb. *Looser 5794*, Santiago (SI); Tarapacá, La Choique cerca de La Tirana, *C. Muñoz Pizarro*, with flowers and fruits, 10 XII 1966 (SGO, SI 26292); Iquique, Pozo Almonte, *Zoellner 3965* (SI).

USES AND PHYSIOLOGY. The tamarugo has been cultivated to some extent, but only in recent years has a real desert-forestation program been started in northern Chile. The "Corporación de Fomento" (CORFO) is planting large areas of desert with this valuable tree, especially for Merino sheep and Karakulor Angora goat raising. Sheep or goats feed on the falling leaves and legumes and occasionally browse the young shoots. It is said that after some years, the planted tamarugo will support 16 sheep per hectare. This is a new development, of which several publications speak enthusiastically (e.g., S. Polanco N., "Los Milagros del Tamarugo," in Patria (2a. Época) 1(3): 23–26. 1967. Santiago de Chile). I have seen photographs by Mario A. Habit C. (from CORFO, January, 1973) showing the transformation of the salt-desert into a dense forest through plantings of tamarugo. Thousands of young seedlings, nursed in seedbeds, are yearly put into the field. Near Iquique, in a nursery, at least 100,000 seedlings were being raised for transplantation in 1970 (Prof. Otto Zoellner, *in litt.* to the author). Polanco writes that every month 150 hectares of desert are planted with tamarugo. He states that the capital put into this forestation is recovered in a period of 9 to 12 years with livestock farming. "It is a unique experience in the whole world, which revolutionizes principles of the live-stock industry" (Polanco, *loc. cit.*, 26). Moreover, sanitary conditions for livestock raising in the desert are excellent. Surely, the tamarugo should be tested in many arid regions of the world.

A very important physiological behavior of this tree has recently been discovered. In the Pampa del Tamarugal it does not rain, and formerly it was thought that the trees could thrive only from subterranean humidity or water currents coming from the western slopes of the Cordillera. However, the investigations of Sudzuki and coworkers have shown that *Prosopis tamarugo* is capable of absorbing the atmospheric humidity, which

is great in northern Chile (owing to the fogs, which are called "camanchacas"). The leaves of this tree absorb water through their stomata when the relative humidity of the air is 95% or more. At night this initiates a flow of sap into the roots and from these into the soil; during the day, the flow reverses. Stomata open mainly at night and are closed in the daytime. (See F. Sudzuki, Absorción foliar de humedad atmosférica en tamarugo, *P. tamarugo* Phil., in Bol. Téc. Estac. Agron. Fac. Agron. Univ. Chile 30: 1–23. *illustr.* 1969; Sudzuki, Botti, & Acevedo, Relaciones hídricas del tamarugo (*Prosopis tamarugo* Phil.) en la localidad de Canchones. *Ibid.* 37: 3–23. 1973.)

The wood of tamarugo is used not only for fuel, but also for furniture, although it is difficult to work on.

Cultivation and a "forest reserve for the tamarugo," considered most important for the Chilean desert, were already demanded more than fifty years ago in an interesting study by the inspector of forests, E. Maldonado (Contr. Estud. Tamarugo, Rev. Chilena Hist. Nat. 22: 65–71. *pls. 3, 4.* Santiago, 1918).

Sect. Monilicarpa Ruiz Leal & Burkart

14. **Prosopis argentina** Burkart, Rev. Arg. Agron. 4: 39. *illustr.* 1937; Burkart, Darwiniana 4: 91. *figs. 6, 7, tab. 13.* 1940; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. Pp. 130, 133. 1952.

Shrub 1.5–2 m. high, laxly branched; twigs cylindric, flexuous, glabrous, reddish when dry, with rather long internodes, the peripheral ones arched downward; axillary shoots elongate, no brachyblasts formed; spines uninodal, axillary, and frequently apical, solitary, absent from many nodes, 0.2–3.5 cm. long. Leaves small, unijugate, puberulous; petiole 5–18 mm. long; stipules very small, triangular, dry; pinnae 1–4.5 cm. long, with 5 to 27 pairs of leaflets, approximate to distant, linear, puberulous to scarcely ciliolate or glabrous, obtuse, nearly enervate, 2.5–5.5 mm. long × 0.6–1 mm. broad. Spikelike racemes axillary, solitary, 4–7 cm. long (including peduncle), with only 20 to 50 florets on pedicels to 1.6 mm. long, all very pubescent; calyx 2 mm.; corolla 5 mm. long, with almost free petals, pubescent outside like the calyx, the tips inside with a few hairs or nearly glabrous; stamens 8 mm. long, the anthers 1.2 mm. long; pistil 1 cm. long, the ovary white, strigose-pubescent, the style glabrous (some florets functionally staminate because of short pistil). Fruit linear-moniliform, bright red when ripe (a color lost in dried specimens), to 13 cm. long, lax, glabrous, with 4 to 14 globose or ovoid segments and very thin, central isthmi; segments 8–12 mm. long × 6–8 mm. in diameter; one suture 2-nerved, the other 3–4-nerved, both broad; faces striate-corrugate; mesocarp thin; endocarp bony, with convex faces and acute extremities; seeds brown, compressed-ovate, 7 mm. long.

Common name. Algarobilla (and several others).

DISTRIBUTION AND ECOLOGY. Endemic in northwestern Argentina in the Andean provinces of Catamarca, La Rioja, San Juan, and northern Mendoza. A typical xerophyte and psammophyte capable of thriving in conditions of extreme drought. Its preference for sand dunes is in marked contrast to that of the common species of *Prosopis* sect. ALGAROBIA, which prefer heavier soils, sometimes salty clay, on lower mesetas, riverbanks, etc. In Catamarca *P. argentina* has been found at elevations of 2000 m.

SELECTED SPECIMENS SEEN (not previously published). **Argentina.** CATAMARCA: Belén, *Sayago 2846* (LIL, SI); Tinogasta, Arenales de Guanchín, *Schreiter 6030* (LIL, SI), *O'Donell & Meyer 5068* (LIL, TEX). LA RIOJA: Arauco, *A. T. Hunziker 4961* (LIL, SI, SP); Quebrada de la Troya, *Covas 1236* (LP, NY); Arauco, *Parodi 14931* (BAA, SI); Quebrada de la Troya, *J. H. Hunziker 2043* (MO). SAN JUAN: El Balde a Adán Quiroga, *Covas 515* and *Ruiz Leal & Roig 18838* (SI); Ullún, *Rodrigo 2843* (SI). MENDOZA: Dept. Santa Rosa, Las Catitas, *Ruiz Leal 11814* (LIL, SI), *15905* (SI).

Sect. ALGAROBIA DC.
Ser. Sericanthae Burkart

15. **Prosopis sericantha** Gillies ex Hooker & Arnott in Hooker's Bot. Misc. 3: 204. 1832 ("1833"); Burkart, Darwiniana 4: 84. *fig. 5a, tab. 8.* 1940.

Aphyllous, horrid, spiny shrub, very similar to species number 16, *P. kuntzei*, but clearly differentiated, smaller, 0.3–2.5 m., rarely to 3.5 m. high; branchlets spiny, shorter and commonly more slender, 0.8–2.5 mm. in diameter. Spikelike racemes shorter, 1.5–4 cm. long, densely pubescent; flowers red, very pubescent on calyx and corolla; pedicels pubescent, to 1.6 mm. long. Fruit linear, more slender, 7–14 cm. long × 0.8–1.3 cm. broad × 6–7 mm. thick; compressed, reddish, endocarp segments hard, closed, subquadrate; mesocarp pasty, bitter.

COMMON NAMES. Temoj; barba de tigre; algarobilla; huaschilla; retama; espina de Dios; albardón.

DISTRIBUTION. Argentina, widely distributed in the western Gran Chaco and Monte regions. To its known area must be added some provinces, such as Salta, Formosa, La Rioja, and San Luis to the south. One incomplete specimen from Corrientes (between Sauce and Perugorría, in bud, without fruits, *Martínez Crovetto & Cherini*, BAB 6119) seems to be this species, but is indicated as a tree and needs confirmation. Small, slender, sterile specimens have been collected in the eastern part of Salta and may be a form of this species or a new related one.

SELECTED SPECIMENS SEEN. **Argentina.** FORMOSA: Ing. Juárez, *Burkart 20233, 20257* (SI). CHACO: Las Breñas, *Venturi 9757* (MO). SANTIAGO DEL ESTERO: entre Torres y Robles, *Bartlett 19735* (GH, NY, SI, UC); Miel de Palo, FCE, *Krapovickas 823* (SI); Beltran, *B. S. Vuilleumier 1029* (GH, SI); Giménez, *Venturi 9695, 10289* (MO). SALTA: Guachipas, Alemanía, 1300 m. elev., *Venturi 9808* (GH, MO, US). CATAMARCA: Dept. La Paz, *Brizuela 15576* (LIL). LA RIOJA: Dept. S. Martín, Bajo Hondo a Pozo Piedra, *Anderson 1534* (SI); Punta de

FIGURE 4. **Prosopis.** Left: Flowering specimens of *P. sericantha*, from wild plants from San Luis, Argentina. Right: Fruiting specimens of same. *Photo.* Dr. Carlos Bruch.

los Llanos, Ruta 38, *B. S. Vuilleumier 1015* (GH, SI). SAN LUIS: 30 km. W of Santa Rosa, Bañado de Cantana, *Burkart 1397.3* (SI); Candelaria, *B. S. Vuilleumier 1014* (GH, SI). MENDOZA: Dept. La Paz, Desaguadero, Paso de las Tropas, *Ruiz Leal 9575* (SI). TUCUMÁN: Leales, Los Puestos, *T. Meyer 12795* (MO); Burruyaco, El Puestito, *Venturi 7651* (MO).

16. **Prosopis kuntzei** Harms in Kuntze, Rev. Gen. Pl. 3(2): 71. 1898; Burkart, Darwiniana **4**: 85. *fig. 5b*, *tab. 9*. 1940; [3] Hassler, Bull. Herb. Boissier, II. **7**: 171. 1907.

Prosopis casadensis Penzig, Malpighia **12**(12): 405. *lám. 9*. 1899.
Prosopis barbatigridis T. Stuckert, Comun. Mus. Nac. Hist. Nat. Buenos Aires **1**(3): 66. *2 tables*. 1899, Pharmazeuth. Post **15**: 1. 2. 9 IV 1899, *Ibid.* **33**: 1–4. 1899.

Subaphyllous, horrid, glabrous tree 4–10(–15) m. high; trunk 40–60 cm. in diameter, much branched, round-topped, consisting mainly of spine-tipped, rigid, straight, cylindrical, multinodal branchlets 8–50 cm. long × 1.2–5 mm. in diameter, glabrous, slightly striate, with small scales on the alternate nodes. Leaves small and falling off very soon in spring after the development of the young shoot, which becomes a spine; petiole

[3] In *fig. 5* (flowers of *P. sericantha* and *P. kuntzei*) the indicated enlargement of × 16 should be corrected to × 10.6.

5 mm.; pinnae unijugate, 1 cm. long; leaflets 3 to 5 pairs, 3–5 mm. long; some leaves reduced to 5 mm. in length and with only 1 pair of leaflets. Spikelike racemes solitary or fascicled, 3–7 cm. long (peduncle 0.5–1 cm.); florets white or yellow, perfumed, glabrous outside; calyx 1 mm.; corolla 3 mm. long, villous within; ovary villous, the style pilose. Legume black, thick, compressed-turgid, straight or subfalcate, mucronate, 10–17 cm. long × 1.5–2.6 cm. broad × 0.6–1.5 cm. thick; pulp mealy-spongy, dry; endocarp segments subquadrate, bony, closed, 1.2 × 1.2 × 0.6 cm.; seed compressed, ovate, brown, with umbo, 7–10 mm. long × 5–6 mm. broad; new shoots with leaves deciduous in July to November; flowering in spring (October to December); ripe fruits from March to May.

DISTRIBUTION. A typical Gran Chaco species of the mixed subxerophilous woods of northern Paraguay and eastern Bolivia to central Argentina (northern Córdoba, Santa Fe, and Corrientes).

COMMON NAMES. Itin; palo mataco; lanza-lanza; jacarandá; carandá; yacarandá; barba de tigre.

MATERIAL EXAMINED. **Paraguay:** Gran Chaco region, Loma Clavel, at 23° 20′ lat. S, *T. Rojas*, Herb. *E. Hassler 2487* (G, MO, NY, SI); Puerto Casado, *Pedersen 4172* (SI). **Bolivia:** Sta. Cruz, Sierra, at 2000 m. elev., *O. Kuntze*, V 1892 (isotype, NY; phototype, Field Mus. 1465, NY, SI); Dept. Santa Cruz, Mairana, 1400 m. elev., *Steinbach 8271* (GH, MO, NY). **Argentina.** SANTIAGO DEL ESTERO: El Charco, *Venturi 9694* (GH, MO, SI), *Schreiter 5948* (LIL, SI); Brea Pozo a Huayco Hondo, *Bartlett 19751* (GH, SI); Lavalle, *Burkart 20360* (SI); E of Quimilí, Route 94, *Solbrig & Vuilleumier 4276, 4279* (GH, SI). FORMOSA: Bartolomé de las Casas, *Solbrig 4244, 4250, 4268*, Las Lomitas, *Solbrig 4260*, west of Bazán, *Solbrig 4262* (GH, SI). CHACO: Colonia Benitez near Resistencia, *Martínez et al.* (BAA 9507, SI); Villa Angela, *Solbrig & Vuilleumier 4280, 4284* (GH, SI). CÓRDOBA: Dept. Totoral, Las Peñas, *Burkart 20100*, Simbolar, *Sayago 2248* (SI).

USES. Heartwood, hard and flexible, bluish-black, specific weight 1.20–1.35; used by the Chaco Indians for bows and spears; at present used for fence-posts because of its resistance to decay, and lumbered for various local uses; said to yield a very valuable timber.

REFERENCES. Record and Hess, Timbers of the New World, 317. 1943; Tortorelli, Maderas y Bosques Argentinos, 403. 1956; Costantino, Arbol Forest. Arg., 1956.

Ser. Ruscifoliae Burkart

17. **Prosopis ruscifolia** Grisebach, Plantae Lorentzianae in Abh. Kön. Ges. Wiss. Göttingen **19**: 82. 1874; Burkart, Darwiniana **4**: 87. *tab. 10*. 1940; Hieronymus, Icon. et Descript. Pl. Arg. **6**: *tab. 2*. 1885.

Spiny, large-leaved, glabrous tree 5–12 m. high, with trunk to 70–90 cm. in diameter; branchlets arched downward, flexuous, green, becoming

dark gray, slender; spines uninodal, solitary, straight, strong, cylindrical, subulate, not at all nodes, 1–33 cm. long, commonly 3–15 cm. long, above their bases 0.6–1.4 cm. in diameter, thicker than the subtending twig. Leaves unijugate, lax; petiole 1–7.5 cm. long; rachis of pinnae 4–11 cm. long; leaflets 2 to 5 pairs, opposite, large, lance-ovate, more or less acute, coriaceous, palmate-pinnatinerved, (2–)4–10 cm. long × 0.7–2.5(–3.8) cm. broad, smooth, not reddish when dry. Racemes 8–15 cm. long (peduncle 1.5 cm. or less), spikelike; rachis and pedicels (1–2.2 mm. long) pubescent or glabrous; florets greenish-yellow, small; calyx 1–1.5 mm., pubescent; petals 3–4 mm. long, glabrous, villous within; stamens 5–7 mm. long; ovary villous. Legume slender, compressed, submoniliform, stipitate and acuminate, subfalcate, straight or S-shaped, 13–29 cm. long × 0.9–1.1 cm. wide, many-seeded; margins undulate, straw-colored, violet-tinged.

COMMON NAMES. Vinal; visnal; quilín; ibopé-moroti. In NE Brazil: Pao de espinho; yuncumarim. In Paraguay: olkhá (in Chamacoco).

DISTRIBUTION. Gran Chaco region, from eastern Bolivia and Paraguay to north-central Argentina (Formosa, Chaco, and Santiago del Estero); a limited area in northeastern Brazil on the boundaries of Piauhy and Pernambuco states in the Catinga (Cachoeira do Roberto, first cited by H. Harms, Notizbl. Bot. Gart. Mus. Berlin-Dahlem **8**: 712. 1924, then by A. Ducke, Legum. Pernamb. e Paraiba, Mem. Inst. Osvaldo Cruz **51**: 429. 1953).

In Argentina, in the western parts of the Gran Chaco, where it invades pastures, it is considered a serious pest, the "plaga nacional" (see discussion below).

SELECTED SPECIMENS SEEN. **Brazil:** Piauhy, Cachoeira do Roberto, *Luetzelburg 49, 1418* (B, NY, US); Pernambuco, Petrolina, Cachoeira do Roberto, 3 km. abaixo da paragem do acude, entre Lago e Sombrío, *Lima & Magalhaes 52–1060* (R 76276). **Bolivia:** Dept.?, Velasco, Seeufer San Pablo, *O. Kuntze*, VII 1892 (NY). **Paraguay:** Dept. Olimpo, Pto. Diana cerca de Bahía Negra, *Arenas 324* (SI); Concepción, *Hassler 7153* (G, GH, MO, NY, UC, US); Curso sup. Río Apa, reg. calcarea, *Hassler 11504* (GH); Pilcomayo River, *Morong 1098* (GH, MO, NY, US); Puerto Casado, *Pedersen 4063* (SI); Bahía Negra, Chaco paraguayo, *Rojas 13720* (SI), *13721* (MO, SI), *13722* (SI). **Argentina.** FORMOSA: La Fidelidad, *Joergensen 2718* (US); Fortín Pilcomayo, *Krapovickas 1207* (GH); Bartolomé de las Casas, *Solbrig 4236, 4237, 4239, 4249, 4266* (GH, SI); Dept. Patiño, *Palacios 307, 313, 321, 326, 332, 335, 478* (BAFC, SI); Las Lomitas, *Solbrig 4259* (GH, SI); Formosa, without further locality, *Maradona 7* (SI). CHACO: Barranqueras, *Curran 79* (MO, NY, US); Dept. Güemes, Ruta 95, *Palacios 489, 498* (SI); Dept. 1° de Mayo, Campo Antequera, *Martínez et al.* (BAA 9564, SI). SALTA: Dept. Anta, Palermo, *Ragonese 76* (SI). TUCUMÁN: Burruyacu, El Puestito, *Venturi 7640* (US); Capital, *Venturi 3819* (US); Leales, Chañar Pozo, *Venturi 5353* (MO, UC, US); Capital, *Lillo 11854* (GH). SANTIAGO DEL ESTERO: Giménez, El Charco, *Venturi 9697*, *Pellegrini & Venturi 5830* (GH, MO, UC, US); Los Telares a Ramírez de Velasco, *Bartlett 19771* (NY); Capital, Parque Aguirre, *López 3* (SI); Arroyo Saladillo, *Sayago 1775, 1778* (SI); Ruta 9, Km. 1012,

borde de salina, *Burkart 20115* (SI); along Route 9, N of Saladillo, *B. S. Vuilleumier 1037* (GH, SI). CÓRDOBA: Dept. Río Seco, Los Hoyos a Villa Candelaria, *Sayago 2203* (SI).

ECONOMIC IMPORTANCE. When full-grown, this tree yields good timber, of the same quality as *Prosopis alba* or *P. nigra*; it is good for flooring, barrels, etc. (L. Tortorelli, Maderas y Bosques Argentinos, 415. 1956). Unfortunately, it grows in regions that are far away from markets and difficult to settle, where primitive cattle-raising is practiced. Owing to the great occupying capacity of *P. ruscifolia*, it is considered a serious pest in the western Gran Chaco region because it colonizes rapidly, forming in its young state dense, spiny, impenetrable thickets where no grass thrives and the livestock industry has to be abandoned. The leaves contain substances capable of reducing or suppressing the germination capacity of other seeds (Souto & Eilberg, Rev. Investigac. Agropecuar. INTA, ser. 2. 9(1): 19–27. 1972. Buenos Aires). The vinal, as noted, has been declared a "plaga nacional." Its behavior reminds one of the "mesquite" problem in Texas. All kinds of livestock and herbivores eat the legumes and propagate the hard seeds of this species endozoically. The seeds germinate much better after passing through the digestive tract, and they are also widely dispersed by the animals. Ranchers believe that a "tropa" of cattle that has been browsing in a vinal-infested area must be in quarantine for 48 hours before being put into a "clean" pasture, so that it will not introduce seeds into the new paddocks. Many experiments have been carried on with herbicides in an attempt to kill the vinal, but they have had only limited success in areas outside the principal infestation regions of the species. Biological control, as far as the writer knows, has not been tried, although it may be the most promising way; however, few, if any, parasites are known on *Prosopis ruscifolia*. I once found heavy infestation of a scale insect or coccid (probably *Lepidosaphes* sp., fam. *Diaspididae*) on my herbarium specimen no. *20115*, collected in 1957 in the province of Santiago del Estero. No field notes on the effect of the parasite on the host were taken, but this scale insect unfortunately seems to belong to a group which attacks important cultivated trees.

18. **Prosopis fiebrigii** Harms, Repert. Sp. Nov. 13: 524. 1915; Burkart, Darwiniana 4: 89. *tab. 11.* 1940.

Tree, apparently unarmed but sometimes with small, solitary or geminate spines 0.2–1 cm. long, otherwise very similar to *P. ruscifolia*, 4–15 m. high; branches flexuous, reddish when dry, the brachyblasts knotty; leaves large, unijugate, glabrous; petiole 0.5–5 cm. long; pinnae (rachis) 6–17 cm. long, with 2 to 9 pairs of opposite leaflets, these coriaceous, pinnatinerved, oval-lanceolate, often undulate or irregularly deformed, 2.5–6.5 cm. long × 0.6–3 cm. broad, emarginate, reddish when dry, obtuse to subacute. Racemes slender, 4–11 cm. long, glabrous, short-peduncled; pedicels 0.2–0.5 mm. long; flowers numerous, small; calyx 1 mm.; corolla 3 mm.; stamens yellowish, 4.5–5 mm. long; ovary white-villous, petals

nearly free, linear, greenish, glabrous but villous within at apex. Legumes subfalcate or straight, long and slender, stipitate and acuminate, similar to those of *P. alba* var. *panta*, 14–29 cm. long × 1.1–1.8 cm. broad, flat-compressed, straw-yellow when ripe; margins nearly straight, parallel; articles up to 23 to 32, subquadrate, compressed, sometimes broader than long, umbonate before ripening; pulp probably edible.

DISTRIBUTION. Paraguay (humid Chaco region); Argentina (Formosa).

MATERIAL EXAMINED. **Paraguay.** CHACO: Puerto Guaraní, barranca riacho, *Rojas 13611* (SI); Puerto Casado, *Rojas* XII 1916 (LIL 54639, GH), *Rojas 2146* (GH), *Pedersen 4064* (SI), *Rojas 8229* (SI). **Argentina.** FORMOSA: Dept. Patiño, El Cogoik, *Palacios 484* (BAFC, SI); Dept. Patiño, Ibarreta, Maruñak, *Quarin & Schinini 441* (CTES, SI); Pilcomayo, *Morel 5006, 6560* (LIL).

OBSERVATIONS. While the closely related *Prosopis ruscifolia* Grisebach, of more western distribution, is known ecologically as a terrible invader of savanna lands in the Gran Chaco, *P. fiebrigii* has not been detected as a nuisance.

19. **Prosopis vinalillo** Stuckert, Anal. Mus. Nac. Buenos Aires 7: 73. *tab. 4.* 1900; Burkart, Darwiniana **4**: 90. 1940.

Tree to 3–10 m. high; trunk 10 to 50 cm. in diameter; branchlets flexuous, in time knotty; foliage glabrous; spines axillary, robust, alternately solitary or geminate, 0.5–12 cm. long, similar to those of *P. ruscifolia* but smaller. Leaves unijugate, large, glabrous, variable as to number of leaflets, these lanceolate or oblong-linear, intermediate in size between *P. ruscifolia* and *P. alba*, in 4 to 12 pairs per pinna, more or less distant on the rachis, coriaceous, penninerved, 10–30 mm. long × 2–12 mm. broad. Racemes spiciform, 6–8 cm. long, like those of *P. ruscifolia*, as are the small flowers; pedicels 0.6–1.5 mm. long. Legume slender, subfalcate, subtorulose, multiarticulate, 6–24 cm. long × 6–12 mm. broad × 3–8 mm. thick, exocarp sprinkled with violet; endocarp segments hard, compressed, subquadrate, with oblique transverse septae; mesocarp pulpy, sweet.

Probable natural hybrid population originated by crosses of *Prosopis ruscifolia* × *P. alba* var. *panta*, as the founder of its name, Don Teodoro Stuckert, rightly supposed. The leaves show evident *P. ruscifolia* affinities, but they have many more and somewhat smaller leaflets; the spines are also intermediate in size and arrangement between those of the putative parents; curiously, on the same twig alternately solitary and paired spines occur, a fact I have also observed on some North American Algarobiae, as stated in the key to the species. The legumes are closer to the *P. nigra* type, but longer.

COMMON NAMES. Vinalillo; algarrobo santiagueño; quilin.

DISTRIBUTION. Argentina, Gran Chaco region (Santiago del Estero, Tucumán, Salta, Chaco, Formosa, and northern Santa Fe); Paraguay

(Chaco). One specimen from Misiones, Argentina, needs confirmation, because up to now no *Prosopis* has been found in that northeastern province.

SELECTED SPECIMENS SEEN. **Argentina.** SALTA: Yuto, Carmelich, *Devoto & Rial Alberti*, Herb. Forestal *1003* (SI). SANTIAGO DEL ESTERO: Río Dulce, *López 4* (SI); Arroyo Saladillo, *Sayago 1770* (SI); Quebrachos, *Sayago 2898* (SI); Dept. Pellegrini, *Venturi 5827, 5828* (SI); Sierra de Guasayán, Choya, *Sayago 2647* (SI); along Route 9, N of Río Saladillo, *B. S. Vuilleumier 1036* (GH, SI); Dept. Copo, Matoque, *T. E. Luna 348* (LIL, TEX); Algarrobal Viejo, Dept. Pellegrini, *F. Luna 362* (MO). CÓRDOBA: Río Seco, *Candelaria & Sayago 158* (SI). CHACO: Güemes, Ruta 95, *Palacios 483, 493, 497, 500* (SI); La Breñas, *Venturi 9758* (GH, MO); Resistencia, *T. Meyer 16274* (US). FORMOSA: Estanislao del Campo, *Maradona 45* (SI); Dept. Patiño, La Primavera, *Palacios 324, 479* (SI); Ing. Juárez, *Bordón 59* (SI).

20. **Prosopis hassleri** Harms, Repert. Sp. Nov. **13**: 523. 1915; Burkart, Darwiniana **4**: 91. *tab. 12*. 1940.

Tree 6–10 m. high, glabrous, unarmed or with a few small, axillary, solitary, or geminate spines; branchlets soon reddish-gray, flexuous, knotty; leaves similar to those of *P. vinalillo*, unijugate, occasionally some leaves bijugate; petiole 1.2–4 cm. long; pinnae 5–19 cm. long; leaflets 6 to 26 pairs per pinna, opposite, ovate-oblong to oblong, obtuse or subacute, subcoriaceous, penninerved, glaucous-reddish when dried, 0.8–4 cm. long × 1.8–7(–16) mm. broad, distant on the rachis more or slightly less than their own width. Spikelike racemes like those in the species group, 6–12 cm. long (peduncle 1 cm.); pedicels 0.5–0.8 mm. long, glabrous or pubescent, as is the rachis; petals (within) and ovary white-villous. Legume of the *P. alba* or *P. alba* var. *panta* type, subfalcate to nearly straight, straw-yellow, compressed, sutures parallel or slightly undulate, stipitate and acuminate, 14–24 cm. long × 1.2–1.5 cm. broad, flat, with 24–33 segments, these subquadrate or rectangular, broader than long; mesocarp pulpy, sweet, edible.

DISTRIBUTION. Paraguay, Argentina, eastern Chaco region, forming open woods of the savanna type.

COMMON NAMES. Algarrobo paraguayo; algarrobo.

SPECIMENS EXAMINED. **Paraguay.** CHACO: Sector López de Felippis, *Rojas 8477* (SI); Sector Puerto Casado, Km. 160, *Rojas 8450*, Asunción, Santísima Trinidad, *Pavetti & Rojas 10807*, L'Assomption, *Balansa 1445*, fruct., 20 XII 1875 (SI); Pilcomayo, inferior, *Rojas 329*, VII 1906 (isotype, P, GH; phototype, Field Mus. 1463, ser. Berlin Mus. 1264); Asunción, *Rojas 14000a* (LIL). **Argentina.** FORMOSA: Dept. Patiño, various localities, *Palacios et al. 311, 320, 322, 325, 462, 467, 468, 480* (BAFC, SI); Pozo de Tigre, *J. Acuña*, Herb. Forestal *1884* (SI); Dept. Pilcomayo, Km. 101, Ruta 11, *Morel 4307* (LIL); Estancia Riacho Negro, *Morel 4045, 4504*, Clorinda, *Rojas 12307* (LIL). CHACO: Fontana near Resistencia, *T. Meyer 1086* (SI).

OBSERVATIONS. This species seems to hybridize in the Patiño area, Formosa, according to field observations made by Ramón A. Palacios and associates in 1972. His collection no. *485* seems to be *Prosopis hassleri* × *P. fiebrigii*; and his collection nos. *466* and *481*, *P. alba* × *hassleri*.

Prosopis hassleri Harms var. **nigroides** Burkart, var. nov.

A var. *hassleri* differt imprimis fructu minori, compresso-moniliformi violaceo-tincto articulis ovato-quadratis subobliquis. Inermis videtur, foliis var. *hassleri* similibus, foliolis circa 8–20 mm. longis × 2–4 mm. latis, distantibus.

TYPE SPECIMEN: **Argentina.** PROV. SANTA FE: Dept. General Obligado, Estancia Las Camelias, *Arturo E. Ragonese 2423*, with ripe fruits, 15 I 1937 (SI).

According to the collector, the heartwood is yellowish-brown; the common name "algarrobo amarillo" is unfortunately the same one as for *Prosopis nigra* var. *ragonesei* Burkart (see below), a species with different leaves and very small leaflets.

This new variety differs from var. *hassleri* by the legume, which resembles *Prosopis nigra* rather than *P. alba*; the leaves in this variety are the same as in var. *hassleri*.

USES. A species certainly worthy of cultivation for shade, timber, and the edible fruits, which are valuable for sweets or forage.

Ser. Denudantes Burkart

21. **Prosopis denudans** Bentham, in Hooker's Jour. Bot. 4: 351. 1842: Burkart, Darwiniana 4: 95. *fig. 8, tab. 14.* 1940.

Spiny shrub 1–2 m. high, glabrous; branchlets flexuous, arched, rather short, hard, grayish with age, knotty; spines always axillary, solitary, hard, light brown, 0.5–4 cm. long. Leaves deciduous, small, glabrous, unijugate; petiole 2–15 mm. long; rachis of the pinnae 6–18 mm. long; leaflets linear, obtuse, 4–13 mm. long, in 1 to 3(to 4) pairs per pinna, the lowest alternate. Racemes axillary or fascicled on brachyblasts, short-peduncled, 2.5–7 cm. long; rachis and pedicels (0.2 mm. long) glabrous; flowers glabrous outside; calyx 1.5 mm. long; petals 3 mm. long, villous within; stamens 5–7 mm. long; ovary villous. Fruit dark reddish-black, shiny when ripe, glabrous or puberulous, very short-stipitate, thick, subcompressed, 2–7 cm. long × 0.7–1.4 mm. broad, typically falcate to annular, with 1 to 1½ open turns and with central hole.

TYPE SPECIMEN. Collected near Puerto Deseado, Santa Cruz, by Middleton (approximately 47° 50′ S latitude).

DISTRIBUTION. Argentina, endemic in Patagonia; an extreme xerophyte adapted to the semidesert shrub steppe with very cold winters (Provinces Neuquén, Río Negro, Chubut, and northern Santa Cruz). The

species reaches nearly 48° S latitude in eastern Santa Cruz, which marks the southernmost limits of the genus.

COMMON NAMES. Algarrobo patagónico; algarrobo de chancho.

SELECTED SPECIMENS SEEN. **Argentina.** PROV. NEUQUÉN: Zapala, R. Castro, *A. Krapovickas 3671* (BAB, SI); Río Picún-Leufú, *Ruiz Leal 16047* (SI); Plaza Huincul, *Cabrera 11003* (LP, SI); Zapala, *Correa, Crespo, & Piccinini 4743* (BAB, SI), *Sayago 3318, 3320, 3326* (CORD, SI); Zapala a Junín de los Andes, *Descole 2224*, R. Salado a Pichi, *Castellanos 20598* (LIL). RÍO NEGRO: El Rincón, Meseta de Somuncura, *Ruiz Leal 25568* (SI); Dept. Valcheta, Pailemán, Sierra Colorada, *Ruiz Leal 25635* (SI); Los Menaccos a Gral. Roca, *Ruiz Leal 25996* (SI). CHUBUT: Dept. F. Ameghino, Uzcudun, leg.? *2078*, Dept. Escalante, Pampa del Castillo, *Crespo & Troncoso 1631* (BAB, SI); Pico Salamanca, *E. De Marco de Kreibohm 236* (SI); Comodoro Rivadavia, *Ruiz Leal 14789*, *Burkart 27576*, Dept. Sarmiento, Laguna Palacios, *Ruiz Leal 25699*, Sarmiento, leg.? *2138* (SI); Dept. Escalante, 100 km. N of Com. Rivadavia, *Eyerdam, Beetle, & Grondona*, Univ. Calif. Exp. Patag. II *23783* (GH, MO, UC). SANTA CRUZ: Dept. Deseado, Bosque Petrificado, *Crespo & Troncoso 1754, 1755*, límite con Chubut, *Ruiz Leal 24140*, Caleta Olivia, *Crespo & Troncoso 1672* (SI).

USES. Wood for fuel; fruit eaten by stock.

OBSERVATIONS. New long shoots in spring (November) are very flexuous and develop the long axillary spines at once, but they produce very few reduced leaves or none at all. Well-developed leaves appear the following year on the knotlike brachyblasts in the axils of the spines in fascicles of 2 to 8.

Prosopis denudans Bentham var. **patagonica** (Spegazzini) Burkart, comb. nov.

Prosopis patagonica Spegazzini, Pl. Patag. Austr., Rev. Fac. Agron. y Vet. La Plata 3(30–31): 510. 1897; Burkart, Darwiniana **4:** 95. *figs. 9, 10.* 1940.

This variety differs from the typical one in the fruits, which are nearly straight, not curved. The difference in number of leaflets given by the original author does not hold true. The fruits measure (2–)4–10.5 cm. long × 0.9–1.3 cm. broad × 0.8–1 cm. thick.

COMMON NAMES. Algarrobillo; espinillo.

MATERIAL SEEN. **Argentina.** MENDOZA: Dept. Malalhue, entre Río Barrancas y Ranquil Norte, *Ruiz Leal 16070* (SI); Río Barrancas, *Burkart 13823* (SI). NEUQUÉN: Loncopué, Churriaca, *Ruiz Leal 18018*; Zapala, 40 km. to the south, *Sayago 3321* (SI); Zapala, *O'Donell 1997* (NY). RÍO NEGRO: Valcheta, *J. L. Alfonso*, Herb. Forestal *2287* (SI); 9 de Julio, Ministro Ramos Mejía, *Pedersen 1664* (US); camino a Somuncurá, *Ruiz Leal 25968* (SI); entre Sierra Colorada y Los Menucos, *Ruiz Leal 26003* (SI); Meseta de Somuncurá, *Roig* (Herb. Ruiz Leal *26071*: SI). PATAGONIA: Santa Cruz, loc.?, at 50° 3′ S latitude, *Moreno & Tonini 453* (NY).

OBSERVATIONS. As I supposed already in 1940, *Prosopis patagonica*

Spegazzini is not a good species and merits only varietal rank. Spegazzini failed to compare it with *P. denudans*.

P. denudans Bentham var. **stenocarpa** Burkart, Darwiniana 9: 75. *fig. 4.* 1949.

Spiny shrub similar to the preceding varieties, differing from them in the slender, thin legume, falcate to annular as in var. *denudans* but only 0.5 cm. in diameter, contracted between the seeds and with more elongated oblong segments, the mesocarp very thin, the seeds 4.5–7 mm. long.

MATERIAL SEEN. **Argentina.** CHUBUT: Dept. Rawson, south of Trelew, *Krapovickas 4367* (holotype, SI). SANTA CRUZ: Dept. Deseado, entre Fitz Roy y Monumento Natural de los Bosques Petrificados, *Ruiz Leal 25681* (SI).

22. **Prosopis ruizleali** Burkart, Darwiniana **4**: 328. *fig. s.n.* 1942.

Spiny shrub 0.6–3 m. high, deciduous, with solitary, axillary spines and gemmiparous horizontal roots (Burkart, *loc. cit.* 331), very similar to *P. denudans* Bentham, but differing in its larger leaves; petioles 0.5–2.5 cm. long; pinnae (1 pair per leaf) 2.5–6 cm. long; leaflets 3 to 9 pairs per pinna, linear, larger, 6–12 mm. long × 1–2 mm. broad, glabrous, distant, the lower ones alternate and the inner lowest often abortive; racemes to 8 cm. long; fruit similar, larger, nearly straight to falcate, 5–17 cm. long × 1–1.5 cm. broad, thick, somewhat compressed; endocarp articles subquadrate to obliquely ovoid; seeds ovoid, 7 mm. long.

DISTRIBUTION. Argentina, Prov. Mendoza, Andes foothills; arid, southern region, where the area connects with that of *P. denudans* Bentham.

SELECTED SPECIMENS EXAMINED. **Argentina.** MENDOZA: Dept. Luján, Estancia El Salto, *Ruiz Leal 21682* (SI); Dept. San Rafael, Volcán Diamante, *Ruiz Leal 17007*, La Faja, 70 km. al N de El Sosneado, *Burkart, Troncoso, & Nicora 13822*, Bardas Blancas, *Burkart, Troncoso, & Nicora 14148*, Malargüe, *Burkart 14802*, Calmucó a Ranquil, *Ruiz Leal 21459* (SI); Calmucó cerca de Ruta 40, *J. H. Hunziker 6376* (BAB, SI); Atuel Valley near El Sosneado, *Böcher, Hjerting, & Rahn 1391* (C, SI). NEUQUÉN: Dept. Pehuenches, Barrancas a Buta Ranquil, *Ruiz Leal 21463*, Ruta 40, *Ruiz Leal 24402*, Chichico Sur, *Ruiz Leal 24506* (SI); Pehuenches, Río Barrancas, Ruta 40, *Ancibor, Cano, & Crespo* (BAB 90181, SI).

OBSERVATIONS. Closely related to *Prosopis denudans* and perhaps not more than a more robust, northern subspecies of it. There is some intergradation in the leaf characters.

23. **Prosopis castellanosii** Burkart, Darwiniana **5**: 66. *fig. 4.* 1941; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas, ed. 2. 130. 1952.

Spiny shrub of horrid, globose appearance, 0.6–1.5 m. high, apparently with a taproot of 15–20 cm. diameter at top; branching basal, with thick woody branches below or on soil surface, procumbent; aerial shoots

hard, flexuous, greenish-glaucous and striate when young, puberulous or glabrescent; internodes short; spines solitary, up to 4.5 cm. long, strong, straw-colored. Leaves small, unijugate, pubescent; petiole to 3 mm. long; pinnae 2–20 mm. long; leaflets small, ovate, subglabrous or puberulous, imbricate or subdistant, 3–12-jugate, 1.6–3.8 mm. long, alternate to opposite. Spikes axillary, short; peduncle and rachis villous or pubescent, 5–16 mm. long; flower head ovate; calyx 1.5–2 mm.; corolla 2.5–3.5 mm. long. Legume oblong-elongate, very flat, lomentoid, reddish-brown, 3.5–8 cm. long × 1.5–2 cm. broad × 0.4 cm. thick, subfalcate, nearly dry; mesocarp thin, the articles subquadrate or broader than long.

DISTRIBUTION. Argentina, endemic in southern Mendoza and northern Neuquén. An extreme xerophyte growing on arid hills at elevations of 600–1300 m.

SPECIMENS EXAMINED. **Argentina.** MENDOZA: Payún-Matrú, *A. Castellanos*, I 1941 (BA 36732; GH, SI, type); Payún-Matrú, Los Ranquiles, *Castellanos 14253*, fruct., 30 I 1941 (LIL). NEUQUÉN: Dept.?, Rincón del Aguila, *Ruiz Leal 24414*, entre Chihuío del Sur y Chihuío del medio, *Ruiz Leal 24510* (SI); Meseta de los Chihuidas, fr. al Cerro Rayoso, *A. Castellanos*, I 1954 (SI); Dept. Picún Leufú, *Ruiz Leal 26850* (SI); Dept.?, Sierra de la Vaca Muerta, camino a Bajada del Agrio, *Castellanos 20587* (LIL).

OBSERVATIONS. Very isolated species within section ALGAROBIA. The flat, lomentoid fruit is very distinct, as is its vegetative habit.

24. **Prosopis calingastana** Burkart, Bol. Soc. Arg. Bot. 6: 223. *fig. 1.* 1957.

Horrid, spiny, low shrub less than 1 m. high, creeping; branchlets very flexuous; internodes short, longitudinally striate, green, becoming cinnamon-brown; spines solitary, strong, 0.4–3 cm. long; leaves small, pubescent, apparently deciduous, unijugate, in axillary fascicles; petioles 0.3–1.7 cm. long; pinnae 0.6–3 cm. long, 4–7-jugate, ovate-elliptic, pubescent, nearly enervate, 3–8 mm. long × 2–3 mm. broad. Racemes 1.5–6 cm. long, axillary; peduncle and rachis pubescent; florets (not yet described) as usual; calyx pubescent, 1–1.5 mm. long; petals nearly free, 3 mm. long, glabrous outside, villous within at the tip; stamens 6 mm. long, the anthers oblong, 0.7 mm. long; apical gland small; ovary stipitate, villous, the style filiform, glabrous. Legume falcate, linear-compressed, 5.5–10 cm. long × 6–9 mm. broad, velutino-pubescent; margins thickened, nearly parallel; faces convex on the longitudinal endocarp segments, these ovate, thin; seeds longitudinal-oblique, mostly 6 to 9, ovate, 8–9 mm. long.

DISTRIBUTION. Argentina, endemic in the Andean regions of San Juan Province at elevations of approximately 2500 m. in arid quebradas of Dept. Calingasta.

COMMON NAME. Cusqui.

MATERIAL EXAMINED. **Argentina.** SAN JUAN: Calingasta, *Moreau & Perrone*, II 1950 (BA 55032; SI, type); Calingasta, Cerro Castaño, Quebrada Amarilla, *Fabris & Marchionni 2278* (CTES, LP, SI); Quebrada del Río Calingasta, *Cabrera, Zardini, & Deginani 24342*, flowering, 15 I 1974 (LP, SI).

OBSERVATIONS. Like *Prosopis castellanosii*, but spikes a little longer and the legume very different, more slender, thick margined, with oblong, longitudinal endocarp segments.

Ser. Humiles Burkart

25. **Prosopis humilis** Gillies ex Hooker & Arnott in Hooker, Bot. Misc. 3: 204. 1832 ("1833"); Burkart, Darwiniana 4: 98. *fig. 11. tab. 15.* 1940; Monticelli, Lilloa 3: 347. *lam. xv, fig. A.* 1938.

Subaphyllous, spiny, erect to prostrate subshrub 20–40 cm. high, of peculiar habit, with thick, short, woody rootstocks and more slender, running rhizomes; aerial shoots rather tender, hardening when mature; stems and spines striate with longitudinal, prominent nerves; spines axillary, geminate, a pair at every node, erect-spreading, 0.5–5 cm. long. Leaves small, reduced and deciduous, less than 1 cm. long, bipinnate, unijugate, with 1 to 3 pairs of glabrous, elliptic, small leaflets or once-pinnate, with only 1 to 2 pairs of leaflets. Spikelike racemes axillary, replacing one of the spines, 3–6 cm. long, showy because of the numerous red florets; petals 5–6 mm. long, glabrous outside. Legume linear, slightly curved, 4–10.5 cm. long × 1 cm. broad, compressed, reddish, with up to 16 subquadrate endocarp segments.

DISTRIBUTION. Central Argentina, endemic in the pampas or open semixerophytic woodlands (in the provinces of Córdoba, San Luis, La Pampa, and SW Buenos Aires); sometimes in rocky or sandy soils. Ornamental, worthy of cultivation as an oddity.

COMMON NAMES. Algarobilla; barba de tigre (and others).

MATERIAL EXAMINED. **Argentina.** CÓRDOBA: Capital, *Lanfranchi 951, A. T. Hunziker 8118* (SI); Dept. Tulumba, S. Pedro, *Sayago 1891* (SI); Villa María a Tío Pujio, *Hunziker 11421*, Río Tercero, *Burkart 13350* (SI); Cañada del Gobernador, a 20 leguas de Córdoba, *Isern 8622* (MA, SI); Pampa de Olain, *Ragonese & Piccinini 9528* (BAB, SI); Dept. General Roca, Huinca Renancó, *A. T. Hunziker 9382* (SI); Dept. Punilla, La Cumbre, *Goodspeed*, Univ. Calif. Andes Exped. II *23242* (GH); Córdoba, without further locality, *Lossen 88* (GH). SAN LUIS: Las Barranquitas a 1000 m. alt., *A. I. Pastore*, Herb. Burkart *6624* (SI). LA PAMPA: Dept. Conelo, E. Castex, *M. Sayago 3198*, Dept. Loventué, Estancia San Jorge, *Cano 4508* (SI); Dept. Caleu-Caleu, Anzoátegui, *Ruiz Leal 25498* (SI); Realicó, *Schulz 5863* (GH); Dept. Capital, Santa Rosa, *Krapovickas 3585* (SI). BUENOS AIRES: Bahía Blanca, *Soriano 525* (SI); Dept. Villarino, 60 km. W of Río Colorado, *Eyerdam, Beetle, & Grondona*, Univ. Calif. Andes Exped. II *23448* (GH, MO, SI).

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FIGURE 5. **Prosopis.** Left: Paratype of *P. rojasiana* (*Rojas 8314*), from Chaco, Margariños, sector Pilcomayo, Paraguay (GH). Right: *P. pallida* (*Mann & Brigham 200*), from Hawaii (GH).

26. **Prosopis rojasiana** Burkart, Darwiniana 5: 70. *fig. 5*. 1941; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. 131. 1952.

Prosopis striata sensu C. Fiebrig & T. Rojas, Ensayo fitogeográfico Chaco Boreal. Rev. Jard. Bot. Paraguay **3:** 83. 85. 1933. Asunción, non *P. striata* Bentham.

Tall, spiny, microphyllous, subaphyllous shrub or tree 2–6 m. high; branchlets slender, striate, glabrous, green; axillary spines in pairs, numerous, long and slender, 1–11.5 cm. long, scarcely striate. Leaves unijugate, deciduous; petiole 0.5–2 cm. long, apically expanded, more persistent than the pinnae, these 1–2.5 cm. long; rachis glabrous, leaflets 8 to 17 pairs, approximate, ciliolate, oblong-elliptic, 1.5–4 mm. long × 0.5–1.2 mm. broad. Spikes slender, 1–5.5 cm. long; peduncle and rachis puberulous; flowers yellow; calyx 1 mm.; petals 2–2.6 mm.; stamens lilac, 4–5 cm. long; ovary stipitate, villous. Legume (not yet described) 4–5 mm. long, 7–8 mm. broad, linear, straight, compressed, reddish, fleshy.

DISTRIBUTION. Paraguay, northern Chaco woods, on clay soils.

MATERIAL EXAMINED. **Paraguay:** Dept. Boquerón, Puerto Casado, *Pedersen 4171* (C, GH, NY, SI, UC, US); Chaco paraguayo, Sector López de Filippis, *Rojas 8310* (SI, holotype); Sector Pilcomayo, Margariños, *Rojas 8314* (GH, paratype; SI).

Ser. Pallidae Burkart

27. **Prosopis rubriflora** E. Hassler, Repert. Sp. Nov. **8**: 552. 1910; Burkart, Darwiniana **4**: 101. *tab. 16.* 1940.

Small tree 5–6 m. high; bark grayish, longitudinally split, permanent; crown flat, the trunk to 25 cm. in diameter; foliage abundant, reminiscent of *Acacia caven* or *Acacia farnesiana*; branchlets moderately flexuous, reddish-brown, knotty; spines axillary, geminate, uninodal, small, 1 cm. long or less, rare, only on new long shoots. Leaves medium-sized, 3–8-jugate, puberulous; petiole 0.3–1.5 cm.; rachis to 3.5 cm. long, crested, with a small annular gland at the junction of every pair of pinnae, these 1–2.5 cm. long; leaflets approximate to imbricate, small, linear, 1.5–3.5 mm. long × 0.4–1 mm. broad, ciliolate, 1-nerved, 11 to 24 pairs per pinna. Racemes spiciform, axillary, much longer than the leaves; rachis with the short, bracteate peduncle, puberulent, 6–16 cm. long; pedicels 0.5–0.8 mm. or less; florets red; calyx 1.5–2 mm. long, puberulous; petals 4–4.5 mm. long, nearly free, pubescent outside, villous within, especially at the tip; stamens and style red, 8–9 mm. long; ovary stipitate, villous. Legume linear, compressed, straight or subfalcate, subtorulose, 9–14 cm. long, 1–1.7 cm. broad, 0.7–0.8 cm. thick, straw-yellow, fleshy; endocarp segments rectangular, hard, in one row as in all Algarobiae; seeds transverse, 6–7 mm. long.

Distribution. Known only from northeastern Paraguay and adjoining southern Mato Grosso, Brazil.

Common name. Espinillo.

New material examined. **Brazil:** Mato Grosso, arroyo Rapadura, en grandes grupos, *Praderi 346*, flowering, 25 VII 1958 (LIL). **Paraguay:** Alto Paraguay, Puerto Risso, Dept. Concepción, *Schulz 8841*, *T. Meyer 18694* (SI); N Paraguay, Centurión, zwischen Apa und Aquidaban, 9 I 1909, *Fiebrig 5348* (isotypes, GH, HBG); Paraguay, without further locality, *Fiebrig 10940* (BAF).

Observations. In its habit, in its small leaves shorter than the racemes, and in its fruit characters, this well-marked species is close to *P. affinis* Grisebach. Its salient peculiarities are the multijugate, Acacia-like leaves and the red flowers.

28. **Prosopis campestris** Grisebach, Plantae Lorentzianae in Abh. Kön. Ges. Wiss. Göttingen **19**: 84. 1874; Burkart, Darwiniana **4**: 111. *fig. 12, tab. 17.* 1940.

Dwarf, much-branched spiny shrub 10–50 cm. high; taproot and short underground branches woody, the aerial branches with short nodes, flexuous, procumbent-ascending, hard; spines uninodal, axillary, paired, divergent, to 4.5 cm. long. Leaves small, 1–2-jugate; petiole plus rachis 3–13 mm. long; pinnae 0.5–3 cm. long; leaflets 6 to 17 pairs per pinna, imbricate, small, oblong, pubescent, 1.5–6 mm. long × 0.6–1.2 mm.

broad. Spikelike racemes cylindric-ovoid, short, 2–3 cm. long, including the peduncle; florets small; calyx and corolla pubescent outside. Legume linear, nearly straight, compressed, subtorulose, 5–8 cm. long × 0.8–1 cm. broad, with 6 to 11 endocarp segments with oblique divisions, 8 × 6 × 3 mm. long, broad, and thick; fruit pubescent when immature.

DISTRIBUTION. Endemic in central Argentina, especially the Sierra region of Córdoba and San Luis. Its presence in Santiago del Estero is doubtful.

COMMON NAME. Algarrobillo.

NEW SPECIMENS EXAMINED. **Argentina.** CÓRDOBA: S. Francisco del Chañar, *Lorentz 2*, fl. & fruit, 2 XII 1871 (GOET, holotype; CORD, NY, isotypes); Dept. Pocho, Taninga, *Luti 4483, 4530* (SI); Dept. San Alberto, *Stuckert 10388* (CORD); Dept. Tulumba, Puerta de Fierro, *Sayago 2139* (SI); Pampa de Pocho, *Ragonese & Piccinini* (BAB 78374, SI); Río Tercero, *Burkart 13349* (SI); Lago San Roque, *A. T. Hunziker 7084* (TEX). SAN LUIS: San Luis a Saladillo, *Burkart 12078* (SI).

OBSERVATIONS. No better characterization can be given of this plant than its extreme dwarfness, which allows the traveller to walk on it, if he does not fear the spines. In the Río Tercero region it is considered a nuisance when agricultural lands are to be won.

The variety *elata* Burkart, *loc. cit.* 1940, has been transferred to specific rank; see *Prosopis elata* (Burkart) Burkart.

29. **Prosopis pallida** (Humboldt & Bonpland ex Willdenow) H.B.K., Nov. Gen. Sp. Pl. **6**: 309 [folio ed.]. 1823; Sprengel, Linn. Syst. Veg. ed. 16. **2**: 326. 1825; M. C. Johnston, Brittonia **14**: 87, 88 [under *P. limensis*]. 1962; Fosberg, Occ. Pap. Bishop Mus. **23**(8): 132–135. 1966.

Acacia pallida Humboldt & Bonpland ex Willdenow, Sp. Pl. **4**(2): 1059. 1805.
Mimosa pallida (Willdenow) Poiret in Lamarck, Encycl. Meth. Bot., Suppl. **1**: 65. 1810.
Prosopis limensis Bentham in Hooker's Jour. Bot. **4**: 350. 1842; Bentham, Trans. Linn. Soc. London **30**: 378. 1875; Burkart, Darwiniana **4**: 114. 1940; M. C. Johnston, Brittonia **14**: 87. 1962; Svenson, Am. Jour. Bot. **33**: 452. *fig. 3.* 1946; Macbride, Fl. Peru [Legum.], Bot. Ser. Field Mus. Nat. Hist. **13**(3): 110. 1943.

ILLUSTRATIONS. O. Degener, Fl. Hawaiiensis **2**: family 169a, *plate s.n.*, 8 V 1937, sub *Prosopis chilensis* (Mol.) Stuntz; Hosaka & Ripperton, Legumes Hawaiian Ranges, Hawaii Agr. Exp. Stat. Bull. **93**: 55. *fig. 34.* 1944 (also sub *P. chilensis*); Svenson, Am. Jour. Bot. **33**: 452. *fig. 3.* 1946, sub *P. limensis*.

Tree (or shrub on sterile soils) 8–20 m. high, trunk to 60 cm. in diameter, unarmed or spiny, with short, axillary, uninodal, geminate, divergent spines less than 4 cm. long. Leaves medium to small in size,

pallid grayish-green when dry, (1–)2–4-jugate, pubescent, ciliolate to subglabrous; petiole short, with the rachis 0.8–4.5 cm. long, pubescent; pinnae 1.5–6 cm. long, with a sessile, cuplike gland at their junction; leaflets green or gray when dry, 6 to 15 pairs per pinna, approximate without touching or a little distant, pubescent or at least ciliolate, oblong-elliptic to ovate, obtuse or mucronate, firm, pinnatinerved below, 2.5–8.3 mm. long × 1.4–4 mm. broad. Racemes spiciform, much (2 to 3 times) longer than the leaves; rachis and the short peduncle pubescent, together 8–15 cm. long; florets dense (200 to 250 per raceme), short-pedicelled, greenish-yellow; calyx ciliolate, 0.5–1.5 mm. long; petals 2.5–3 mm. long, free, villous within; stamens 5–7 mm. long; ovary stipitate, villous. Legume straight or subfalcate, very similar to that of *P. juliflora* (Sw.) DC., but thicker, straw-yellow when ripe, with parallel margins, fleshy, sweet, edible, subcompressed, long or short stipitate with rounded base, and acuminate, sometimes nearly subquadrate-rectangular in transection, (6–)10–25 cm. long × 1–1.5 cm. broad × 5–9 mm. thick; endocarp segments to 30, broader than long; seeds oblong, brown, 6.5 mm. long.

COMMON NAMES. Algarrobo or algarroba, algarroba paiva, huarango (Peru); algarrobo americano (Puerto Rico); kiawe, algaroba, mesquite (Hawaii); carobier (Marquesas).

DISTRIBUTION. Native to Peru, Colombia, and Ecuador in the drier parts and along the Pacific coast; naturalized in some parts of Puerto Rico, very much so in the Hawaiian Islands, and perhaps elsewhere (Brazil); introduced for cultivation in India and Australia.

MATERIAL EXAMINED. **Colombia:** Intendencia del Meta, Llanos orientales, Cumaral, at 280 m. elev., *García-Barriga 4976* (LIL). **Ecuador:** Prov. Oro, Machala to Puerto Bolívar, *Hitchcock 21114* (NY); Prov. Loja, Puente Boquerón, *Asplund 18078* (NY, R); Catamayo Valley, La Toma, *Wiggins 10950, 10953* (NY); Durán, *Rose & Rose 23587* (NY); Prov. Guayas, Guayaquil to Salinas, at sea level, *Mexía 6739* (NY). **Peru:** Prov. Piura, Paita, *Rose 18511, Williams 2923, 2974* (NY); Pariñas Valley, *Haught 164* (NY); Lima(?), Río Apurimac, *Weberbauer 5901* (NY); Dept. Arequipa, Caravelí, Lomas, *Iltis & Ugent 1586* (NY); Jard. Bot. Lima, *O. Velarde N. 2730* (CORD, SI); Puente de Olmos, *Angulo & López 405* (SI); Dept. Ica, laguna de Orovilca cerca de Ica, *Ferreyra 2498* (SI, US), *O. Velarde N. 1537* (LIL); Prov. Lambayeque, Olmos, *O. Velarde N. 812* (LIL). **Puerto Rico:** Mayaguez, Cabo Rojo, *Stimson 3132* (MO, NY, UC); Distr. Mayaguez, Cabo Rojo, El Combate, *Burch 6678* (MO). **Hawaiian Islands:** Oahu, Honolulu, dry coral plain, *Baker 128* (BISH); Waikiki, *Hastings*, 28 IV 1931, Lower Diamond Head, *St. John & Christophersen 10552* (BISH, SI); Honolulu, *Fosberg 14217* (NY), *Fosberg 42015* (US); University of Hawaii, Manoa Campus, *Solbrig 4225* (GH, SI), *D. Herbst 539* (BISH, SI); Oahu, *Degener 7263, Harris C-242149, Heller 2001* (MO, NY), *Long 1706* (US); Nanakuli, *Degener 9955* (MO, US); Molokai, *Hitchcock 15114* (US). **Marquesas Islands:** Uahuka, *Decker 1908*, introduced from Hawaii (US). **India:** Lahore, Laurence Gardens, fl., fruct., V 1912 (GH). **Australia:** Queensland, Brisbane, cultivated Botanic Gardens, *C. T. White 2390, 8642* (GH).

OBSERVATIONS. I could not find any constant difference between *Proso-*

pis pallida and *P. limensis* and therefore place the latter name into the synonymy of the former. Both species were described originally from Peru, and Bentham, the author of *P. limensis*, neglected to compare it with the much earlier *P. pallida*.

Fosberg (*loc. cit.* 1966, p. 134) distinguishes *Prosopis pallida* forma *pallida*, unarmed, and forma *armata*, with spines. In Hawaii he found that nearly ¼ or ½ of the trees of different forests were spiny and the rest were spineless. No study of this sort has been made in the original home of the species, where it is not yet cultivated. Probably the spiny type dominates. Herbarium specimens are not conclusive in this respect, because not all branchlets of a tree may be spiny.

Previous to M. C. Johnston's discussion of this species (Brittonia, 1962), it had been neglected and, especially in Hawaii, was treated as *P. juliflora* or *P. chilensis*.

In the tropical rainforest of Ecuador, near Santo Domingo de los Colorados, 40 km. from Quevedo, at 570 m. above sea level, there appears an intermediate form, *Prosopis pallida* × *P. juliflora*, with the following characters: trees to 30 feet tall; flowers white; spines rare, geminate, to 2 cm. long; foliage glabrous; leaves bijugate, expanded; leaflets oblong, 8–11 mm. long, glabrous, somewhat distant; pinnae to 6.5 cm. long, as in *P. juliflora*; racemes longer than the leaves, up to 15 cm., as in *P. pallida*. Perhaps this is a form of *P. juliflora* var. *horrida*.

USES. *Prosopis pallida* is a very valuable tree for ornament, for shelter in arid conditions, and for timber, fuel, and forage (fruits). It is highly esteemed by foresters in Hawaii. Its cultivation must be encouraged in other warm and dry countries. See W. L. Hall, The forests of the Hawaiian Islands. U. S. Dept. Agr., Bur. Forestry Bull. **48**: 9, 10. 1904. Washington, D. C. ("Algaroba" forests, sub *Prosopis juliflora*); Hosaka & Ripperton, *loc. cit.*; Degener, Fl. Hawaiiensis **2**: 1937 (sub *P. chilensis*).

If Fosberg (Occ. Pap. Bishop Mus. **23**(8): 132–135. 1966), following Johnston (1962), is correct that the Hawaiian "algaroba-forests" are formed by *Prosopis pallida*, then the following paper must be considered here: Hosaka & Thistle, Noxious Plants of the Hawaiian Ranges, Ext. Bull. Univ. Hawaii **62**: 23. 1954 (sub *P. chilensis*). The authors do not deny the utility of the tree, but they maintain that it may become an invader and form thickets which are a nuisance.

30. **Prosopis affinis** Sprengel, Linn. Syst. Veg. ed. 16. **2**: 326. 1825. Göttingen.

Prosopis algarobilla Grisebach, Plantae Lorentzianae in Abh. Kön. Ges. Wiss. Göttingen **19**: 83. 1874; Burkart, Darwiniana **4**: 115. *fig. 13.* 1940, and **3**: 28, 40, 114. *tab. 2.* 1937, 1939.

Prosopis nandubey Lorentz ex Grisebach, Symb. Fl. Argent. in Abh. Kön. Ges. Wiss. Göttingen **24**: 117. 1879.

Prosopis algarobilla Grisebach var. *ñandubay* (Lorentz) Hassler, Repert. Sp. Nov. **16**: 154. 1919; Burkart, Darwiniana **4**: 118. *tab. 18.* 1940.

FIGURE 6. **Prosopis.** Lectotype of *P. affinis* (*Sello s.n.*, circa 1825), Montevideo, Uruguay (MO).

Flat-topped, spiny savanna tree of medium or small size, 2–8 m. high, much and irregularly branched; bark persistent, grayish, fissured; trunk short, to 50–60 cm. in diameter; branchlets somewhat flexuous; geminate,

axillary spines short, divergent, 0.3–2.5 cm. long. Leaves persistent, small, 1–3-jugate, petiole (incl. rachis) 0.2–2.2 cm. long; pinnae 1–6 cm. long; leaflets small, glabrous or puberulous, approximate to imbricate, 10 to 30 pairs per pinna, linear-oblong, firm, obtuse to subacute, pinnately reticulate-nerved below and on the margins, greenish when dry, 2–7.5 mm. long × 0.8–1.8 mm. broad. Racemes spiciform, longer than the leaves, short-peduncled; rachis long, pubescent (with peduncle), 5–13 cm. long; florets greenish-yellow; calyx puberulous, 1.5 mm. long; petals 4 mm. long, also pubescent outside, villous within; ovary stipitate, villous; stamens 7–8 mm. long. Legume falcate to annular, rarely straight or S-shaped, linear-oblong, compressed; margins undulate, therefore moniliform, 7–17 cm. long × 0.9–1.6 cm. broad × 6–8 mm. thick; exocarp crustaceous, straw-colored, much tinged with red or violet, sometimes entirely dark-violet; mesocarp thin, pulpy, acidic; endocarp segments 8 to 19, hard, flattened, ovate-rotund to subquadrate, variable, 7–10 mm. long × 7–14 mm. broad × 3–4 mm. thick.

DISTRIBUTION. Bolivia(?), extreme southern part; Paraguay; eastern Argentina, north of Buenos Aires; Brazil, extreme SW of Rio Grande do Sul; western Uruguay. An important campos-tree, forming light forests with herbaceous understory rich in grasses.

COMMON NAMES. Ñandubay; espinillo; algarrobillo; espinillo ñandubay; ibopé-morotí (guaraní name); algarrobo ñandubay.

SELECTED NEW MATERIAL EXAMINED. **Brazil.** RIO GRANDE DO SUL: Uruguaiana, Barra do Quarai, *Rambo 4215, 26354* (LIL, SI). **Paraguay:** Concepción, Puerto Risso, *Meyer & Schulz* (LIL 471409); Chaco, Estancia Peña, *Rojas 14032* (LIL, MO, SI); Curupaytí, *T. Meyer 15956, 15957* (LIL); Ypacaray, *Sparre & Vervoorst 2334* (GH, LIL), *Hassler 3490* (GH); Itapé, *Joergensen 4561* (GH, MO), *Hort. Paraguar. 9071* (SI); Chaco, Loma Clavel, *Hassler 2483* (MO); Central Paraguay, *Morong 851* (MO), *Hassler 12392* (MO). **Argentina.** FORMOSA: Clorinda, *Rojas 12302* (GH); Laguna Oca, *Rojas 12227* (SI); Dept. Patiño, *Palacios 333, 463* (BAFC, SI); Dept. Monteagudo, Dalmacia, *Krapovickas et al. 13826, 13831* (CTES, SI). CHACO: 25 de Mayo, Napalpí, Campo Largo, *Buratovich 572, 612* (LIL); Barranqueras cerca de Resistencia, *T. Meyer 16272* (SI); Fontana, *Meyer 3814* (GH, LIL, NY); Las Breñas, *Venturi 9765* (GH, MO, NY). CÓRDOBA: San Justo, costa de Mar Chiquita, *Sayago 3623*; S. Francisco a Devoto, *Sayago 3577, 3625* (SI); Concepc. del Tío a Mar Chiquita, *Kurtz 12916* (CORD, SI); Río Tercero, Corralito, *Sayago 3681, 3682* (CORD, SI). SANTIAGO DEL ESTERO: Dept. Moreno, Girardet, *J. Morello* VII 1964 (SI 29956). SANTA FE: Dept. S. Cristóbal, E. Rams a Hersilia, *Krapovickas 693, 741* (SI); Dept. S. Javier, Alejandra, *G. Martinez Achenbach 992* (SI). CORRIENTES: Capital a Mburucuyá, *Burkart 27822* (SI); Goya, *Boelcke 1535* (SI); Paso de los Libres, *Ibarrola 2222* (NY); Monte Caseros, *Ibarrola 2415* (GH); Empedrado, La Yela, *Pedersen 3071* (MO). ENTRE RÍOS: La Paz, *Burkart & Bacigalupo 21231* (SI); Concepción del Uruguay, *Lorentz 896* (GH, FI, isotypes of *P. ñandubey* Grisebach), *L. Hauman* (BA 51388), *Nicora 3176* (SI); arr. Isletas, *Burkart 21754, 21756, 21758* (SI). Gualeguaychú, *Burkart 27699* (SI). BUENOS AIRES: Partido Escobar, B. de Escobar, *Burkart 23903* (SI). **Uruguay:** Paysandú, Chapicuy,

Rosengurtt B-3653 (LIL, SI); Dept. Colonia, Estancia Recreo, *Bartlett 21241* (UC, US); probably western Uruguay, Montevideo, *F. Sellow*, sub *P. affinis*, ex Bernhardi Herb. (MO 1844461, lectotype specimen).

USES. *Prosopis affinis* yields valuable fuel and highly esteemed fence posts of great durability (in fact, it is the most valuable tree for that purpose). In many "estancias" (ranches) its use is rationed; it is cut down after 8 to 10 years and allowed to regenerate in lands of mixed forest/stock-raising industry. In open stands this *Prosopis* allows a vigorous grass-sod to grow among the trees; at the same time it offers shelter and, with the fruits, a concentrated food to cattle (which is welcomed in summer when grass grows more slowly). The flowers serve as an excellent bee-pasture.

This species is to be recommended for reforestation. According to my own experience at the botanical garden of the Faculty of Agronomy, Buenos Aires (1928 to 1943), where the species is cultivated from Chaco seed, it was full-grown and matured fruits for the first time at 7½ years of age (3.5 m. high; trunk 7.5 cm. in diameter). Its growth rate is therefore not as slow as many people believe (Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. 135. 1952. Buenos Aires).

In Uruguay it is also important as a forest tree and has been the subject of a special study by Professor Marta Rolfo, Montevideo (ined., in SI).

OBSERVATIONS. The binomial *Prosopis affinis* Sprengel was a taxonomic mystery for a long time, owing to the brevity of the original diagnosis and the impossibility of finding the type specimen. In my earlier paper I had to leave it within the *nomina dubia* (Burkart, Darwiniana 4: 125. 1940). Fortunately, this year I discovered a probable isotype in the herbarium of the Missouri Botanical Garden. It arrived there with the J. J. Bernhardi Herbarium purchase made in Germany by Henry Shaw, founder of the Garden in the year 1857. Bernhardi's herbarium contains specimens collected in Brazil and Uruguay by Friedrich Sellow (or Sello) in the years 1820 to 1831. His specimen is marked "*Prosopis affinis* Spr., Montevideo," but it probably comes not from that city, but from western Uruguay, where the species is common and where Sellow collected (see his travel routes described by Ignatz Urban in Martius's Flora Brasiliensis. Vol. 1. 1906). Bernhardi's specimen may become the lectotype of *P. affinis* Sprengel, a name which must replace the long-known *P. algarobilla* Grisebach.

The specific epithet alludes to the affinity of the species with the preceding one in Sprengel's enumeration, *P. pallida* (Willdenow) Kunth, which indeed is its nearest relative even now.

31. **Prosopis articulata** S. Watson, Proc. Am. Acad. **24**: 375. Jan. 31, 1889; Burkart, Darwiniana **4**: 103, 113. 1940; Johnston, Brittonia **14**: 86. 1962.

Neltuma articulata (S. Watson) Britton & Rose, N. Am. Fl. **23**(3): 187. 1928.

Prosopis juliflora (Swartz) DC. var. *articulata* (S. Watson) Wiggins, Contr. Dudley Herb. **4**(2): 17. 1950; Shreve & Wiggins, Vegetation and Flora of the Sonoran Desert **1**: 604. 1964.

Neltuma pazensis Britton & Rose, N. Am. Fl. **23**(3): 187. 1928.

Prosopis pazensis (Britton & Rose) Wiggins, Contr. Dudley Herb. **4**(2): 18. 1950; Shreve & Wiggins, Vegetation and Flora of the Sonoran Desert **1**: 605. 1964.

Upright polypodial shrub 2–5 m. high or tree with short trunk; bark smooth, brown; branchlets flexuous, greenish; spines axillary, uninodal, paired, rarely solitary, 0.3–3 cm. long; foliage puberulous or glabrous, shorter than the racemes. Leaves unijugate, rarely uni- or bijugate on strong shoots, and then sometimes equalling the racemes, small on brachyblasts; petioles 0.2–2.5 cm. long; pinnae 0.4–6.5 cm. long; leaflets 6 to 20 pairs, linear-elliptic, obtuse, small, 2.5–12 mm. long × 1.2–3.5 mm. broad, approximate on the rachis or a little distant, less than their own width, glabrous or puberulous, enervate, unicostate or reticulate-nerved. Racemes 4–9 cm. long, longer or equalling the leaves; florets small, numerous, yellow, and similar to all those of the *P. juliflora* group; pedicels short; petals free, 3.5–4 mm. long, villous at the apex; ovary stipitate, pubescent. Legume dry, moniliform in outline but very much flattened, yellow or tinged with violet, 10–24 cm. long × 5–8 mm. broad, the segments elliptic-fusiform, longitudinal, 5 to 18; stipe 1–3 cm. long; isthmi narrow, 1–5 mm. broad; pericarp thin (0.2–0.5 mm. thick at maturity); exocarp puberulous or glabrous, striate; mesocarp longitudinally fibrous; endocarp thin, flexible, smooth, whitish, the segments 1–1.8 cm. long. Fruit of bitter taste, not sweet as in common species (*teste* M. Martínez); seeds longitudinal, elliptic, brown, 7–8 mm. long, funicle short, coiled, fixed at the distant angle of the segment.

COMMON NAMES. Mesquite amargo; mesquit; mezquite.

DISTRIBUTION. Northwestern Mexico (Sonora, Baja California) and perhaps Arizona, U.S.A. Flowering and fruit setting in November. Stony and sandy mesas or plains.

MATERIAL EXAMINED. **Mexico.** SONORA: Guaymas, stony mesas at foothills, Sept. 1887, *E. Palmer 197* (GH, holotype; NY, UC, US, isotypes); Guaymas, *Gentry 4689* (GH; MEXU; UC, topotype; US); Guaymas, *J. N. Rose 1224* (MEXU, US); Hermosillo, *Maltby 250* (US); Bacum Station, near Río Yaqui (south of Guaymas), Pacific slope, *Pennell 20204* (GH, NY, US). BAJA CALIFORNIA: Cape District, *Peters 108* (UC); Sierra de la Giganta, *Carter 4135a* (UC); San Nicolás Bay, *I. M. Johnston 3708* (US); Puerto Escondido, *I. M. Johnston 4137* (US); San Evaristo Bay, Gulf of California, *I. M. Johnston 4087* (MO, US); La Paz, *Martínez 26* (US), *J. N. Rose 1324* (GH, isotype of *Neltuma pazensis*); Valle de la Paz, *E. Mayoral Vazquez 3280* (ENCB). **United States(?).** ARIZONA: Phoenix, *H. Hubbard*, 13 IV 1930 (COLO 46104).

OBSERVATIONS. This is, according to M. C. Johnston (Brittonia **14**: 86), "one of the more distinct taxa in a group of indistinct ones." Some specimens, such as those collected by Ivan Johnston in Sonora, have

FIGURE 7. **Prosopis.** Flowering and fruiting branchlet, × ½, of *P. elata* (*Rojas 8323*), from Chaco, Puesto Buenos Aires, sector Pilcomayo, Paraguay (SI).

larger leaves and leaflets than usual, but a typical *articulata*-pod. They may indicate a *Prosopis laevigata* or *P. velutina* introgression.

Hybridization seems to occur with *P. velutina*, a species growing in the same Sonoran regions; for instance, *White 402* is assigned here to *P. velutina*, but has fruit characters tending toward *P. articulata*.

Variation of leaf size shows a dimorphism connected with the existence of long and short shoots. In *Gentry 4689* I measured on the same branchlet:

a) on brachyblasts — petiole 0.5–1 cm. long; pinnae 0.4–1.2 cm. long; leaflets 6 to 13 pairs per pinna, 3.5–5 mm. long.

b) on megablasts — petiole 1–2.5 cm. long; pinnae 3.5–4 cm. long; leaflets 12 to 13 pairs per pinna, 7–9 mm. long.

32. **Prosopis elata** (Burkart) Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. 131, 544. 1952.

Prosopis campestris Grisebach var. *elata* Burkart, Darwiniana **4**: 112. 1940.

Spiny shrub 0.6–4 m. high, polypodial, arborescent; bark dark; branchlets flexuous, green, knotty, with short internodes; small leaves; spines axillary, uninodal, geminate, smooth, variable, 0.5–8.5(–11.5) cm. long, 3–4 mm. in diameter, the exceptionally long ones to 5 mm. in diameter near the middle, strangled at base, thicker than the supporting branchlet, often perpendicular to it, rarely solitary. Leaves uni- to bijugate; petiole (including rachis) 0.5–3.5 cm. long; pinnae 1.5–3.5 cm. long; leaflets 15 to 26 pairs per pinna, approximate, their margins touching or less distant than their width, puberulous or glabrous with ciliae at the base, elliptic-oblong, obtuse or subacute, pinnatinerved, 2–4.5(–6) mm. long × 0.7–1.2 mm. broad. Racemes spikelike, 2–7 cm. long, laxi- or densiflorous; florets puberulous or glabrous outside, greenish-white to yellow, sometimes reddish; petals villous at apex, 2–3 mm. long. Legume straight, fleshy, compressed, yellow, tinged with violet, 6–9 cm. long × 6–8 mm. broad, puberulous when immature; margins undulate; segments subquadrate, 11–13; pulp acid, not edible, scarce.

DISTRIBUTION. Paraguay, Argentina, Gran Chaco, especially abundant in the central Pilcomayo region, forming open woods of the savanna type.

COMMON NAMES. Algarrobito; algarrobillo; huaschillo; guaschin (Formosa, *teste* J. Morello); quisca-taco (Formosa, *teste* Bordón); guajchillo (Santiago del Estero); ixwinúk (Salta, *teste* Métraux, Mataco Indians).

NEW MATERIAL EXAMINED. **Paraguay:** Sector Pilcomayo, Muñoz, *Rojas 6978* (SI). **Argentina.** SALTA: Dept. Orán, Pichanal, Carmelich, *Devoto & Rial Alberti*, Herb. Forestal *1007* (SI); Salta, chaco, Selva San Andrés, *Métraux*, sterile, 17 IV 1939 (US). LA RIOJA: Dept. Tello, *Ruiz Leal & Roig 17210* (SI). TUCUMÁN: Dept. Leales, Las Herreras, *Monetti 1211* (LIL, SI). FORMOSA: Ing. Juárez, *Burkart 20201*, *Bordón 60* (SI); Fortín Pilcomayo, *Krapovickas 1240* (LIL, SI); Estero Patiño, *Morello & Adámoli* V 1967 (SI). SANTIAGO DEL ESTERO: Dept. Río Hondo, Va. Jiménez, *Venturi 9712* (MO, NY, US); Dept. Giménez, El Charco, *Schreiter 5959* (LIL, SI); Espada, *Argañarás 364* (SI). CÓRDOBA: Dept. Tulumba, Puesto de Fierro, *Sayago 2161* (SI); Dept. S. Justo, Marull, *Sayago 1690, 1764* (SI); Dept. Río Seco, Villa Candelaria, *Sayago 46* (SI).

USES. According to Métraux, *in schedula*, the wood is used for making bows.

33. **Prosopis tamaulipana** Burkart, nom. nov.

Neltuma palmeri Britton & Rose, N. Am. Fl. **23**(3): 185. 1928 (not *Prosopis palmeri* S. Watson, 1889).

Trees of small to medium size, round-topped; trunk short; old bark

rough and gummy; branchlets drooping (as in willows), green, slender, slightly flexuous and knotty, the young ones 2–3 mm. in diameter; spines geminate, axillary, short, 0.5–1.5 cm. long, not present on all nodes. Leaves mostly fascicled, uni- to trijugate, glabrous or puberulous, glaucous-grayish when dry; petiole (plus rachis when present) 0.4–3.5 cm. long, pubescent or glabrous; pinnae 2.5–4 cm. long; leaflets (15 to) 20 to 29 pairs per pinna, approximate on the rachis, oblong, obtuse, grayish-green, glabrous, puberulous or with more or less marginal ciliae, 2.8–5(–7) mm. long × 1–1.8 mm. broad, pinnately reticulate-nerved below. Racemes 5–8 cm. long; flowers small, greenish-white; pedicels 0.5–0.8 mm. long; calyx ca. 1–1.5 mm.; petals 3–3.5 mm.; stamens 5–6 mm. long; ovary villous. Legume straight, 8–13 cm. long × 6–8 mm. broad, linear, compressed-submoniliform, puberulous or glabrous, straw-yellow with longitudinal striae; stipe 6–8 mm.; acumen 2–10 mm. long; margins somewhat constricted between the seeds; mesocarp pulpy, sweet; endocarp segments 10 to 18, hard, coriaceous, closed, ovate-rhombic to obliquely subquadrate, ca. 5.5 × 6–6.5 × 3.5 mm. long, broad, and thick; seeds ovate, compressed, brown, 5–5.5 mm. long.

DISTRIBUTION. Mexico: Tamaulipas and Veracruz.

MATERIAL EXAMINED. **Mexico.** TAMAULIPAS: vicinity of Victoria, at ca. 320 m. alt., *E. Palmer 400*, V VI 1907 (GH, MO, isotypes of *Neltuma palmeri* Britton & Rose; NY); Valle de los mamuts, 10 km. al N de Xicoténcatl, 100–200 m. elev., perfil através de Sierra Madre Oriental, región de Gómez Farías, *Martín & Saravia 1141* (ENCB); Altamira, *Crutchfield & Johnston 5230* (TEX); Ejido Guemez, 300 ft. elev., on alluvial clay flat, very common trees. *Crutchfield & Johnston 5181* (MEXU). VERACRUZ: 9 miles east of Ébano, S.L.P., brush on heavy clay, elev. 50 ft., *Crutchfield & Johnston 5146* (TEX).

Ser. Chilenses Burkart

34. **Prosopis chilensis** (Molina) Stuntz emend. Burkart

Ceratonia chilensis Molina, Saggio sulla storia naturale del Chili 172. 1782; Hauman, Physis **7**(24): 75. 1923.

Prosopis chilensis (Molina) Stuntz, Invent. Seeds Pl. Import., U. S. Dept. Agr. Bur. Pl. Industr. **31**: 85. 1914 (cf. Index Kew. Suppl. VI; Gray Herb. Index); Burkart, Darwiniana **4**: 105. 1940; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas, ed. 2. 131. 1952; Benson, Am. Jour. Bot. **28**: 749. 1941; Looser, Rev. Univ. Catól. Chile **47**: 103–116. 1962; Johnston, Brittonia **14**: 88. 1962.

Acacia siliquastrum (Cav.) Lagasca, Gen. Sp. Pl. 16. 1816.

Prosopis siliquastrum (Lagasca) DC. Prodr. **2**: 447. 1825.

Prosopis schinopoma T. Stuckert, Bull. Acad. Geogr. Bot. III. **13**: 87. 1904.

ILLUSTRATION. C. Muñoz P., Sinopsis Flora Chilena 153. *pl. 132*. 1959.

Tree, becoming large in age, with short trunk, 3–10 m. tall, the treetop rounded; branchlets flexuous, knotty, partly spinous; spines on strong shoots, axillary, geminate, uninodal, hard, conic-subulate, up to 6 cm.

long. Leaves deciduous, glabrous, uni- to bi- or trijugate, elongate, but giving only slight shade, mostly fascicled; petiole (rachis when extant included) 1.5–12 cm. long; pinnae 8–24.5 cm. long; leaflets 10 to 29 pairs per pinna, long-linear and distant on the rachis (4–12 mm. apart), glabrous throughout or with some ciliae on the margins at base, 1.1–5.4 cm. long × 1.1–3 mm. broad, pale green, nearly enervate or only the costa prominent, but not of a different color. Racemes spiciform, densiflorous, ca. 7–12 cm. long; flowers as usual, greenish-white to yellowish, ca. 250 per raceme; calyx 1 mm.; petals 3 mm. long, villous within; stamens 5–6 mm. long; ovary pubescent. Legume linear, compressed, with parallel margins, straw-yellow, stipitate and acuminate, nearly straight, falcate or subfalcate, ca. 12–18 cm. long × 1–1.8 cm. broad × 0.6 cm. thick; mesocarp sugary, edible; endocarp segments transverse-rectangular, broader than long, subcoriaceous, easy to open, numbering 20 to 32; seeds ovoid, compressed, brown, 6–7 mm. long.

DISTRIBUTION. A variable species, its natural area extending from Peru and Bolivia to central Chile (type locality: vicinity of Santiago) and northwestern Argentina (the provinces of Salta, Tucumán, Catamarca, La Rioja, San Juan, Mendoza, San Luis, and Córdoba). A detailed account, geographical and historical, on the distribution of this important tree is given by G. Looser, Rev. Univ. Catól. Chile 47: 103–116. 1962, for the province of Santiago, Chile. In southern Peru it is found at elevations of up to 2900 m.

COMMON NAMES. Algarrobo de Chile; algarrobo; algarrobo blanco; algarrobo panta; árbol blanco (Argentina). Algarrobo, tcako, cupesi (Bolivia, *fide* Cárdenas, Not. Prelim. Mat. Medica Boliv. 13. 1943, sub *P. juliflora*).

NEW MATERIAL EXAMINED. **Peru:** Cuzco, Hacienda Potrero, Convención, *César Vargas C. 2041* (MO, SI); Prov. Calca, Hoco, *C. Vargas 709* (MO). **Bolivia:** Dept. Santa Cruz, San Rafael bei San Ignacio and San Ignacio, *Schmidt 102, 136*, Oct. 1951 (SI). **Chile.** COQUIMBO: Dept. Elqui, Algarrobal y Huanta, *Looser 4333, 4483* (SI); Ovalle, Tongay, Quebrada Salina, *C. Jiles 1651* (LIL); Ovalle, *C. Jiles 509* (SI), *Wagenknecht*, Herb. *Looser 4502*, III 1942 (SI); Dept. Elqui, Río Turbio, 1200 m. elev., *Wagenknecht*, Univ. Calif. Andes Exped. II *18477*), Vicuña a La Serena, *Worth & Morrison*, Univ. Calif. Andes Exped. II *16346* (MO, UC); Dept. Illapel, Hacienda Chillepin, *Looser 2224* (GH). ACONCAGUA: Putaendo al N de Los Andes, *Zoellner 4934* (SI); San Felipe, *Killip & Pisano 39781* (SI). SANTIAGO: Tiltil, *Montero 82* (GH), *Senn 4534* (MO, NY, UC); Polpaico, *B. K. Cassels* (SI 26960); Batuco, *Hastings 350* (UC). **Argentina.** TUCUMÁN: Dept. Tafí, Amaicha de Valle, 2300 m. elev., *Burkart 5486* (SI). SANTIAGO DEL ESTERO: Capital, very rare, *Argañarás 466* (SI). CATAMARCA: Belén, *Devoto et al.*, Herb. Forestal *645, 651* (SI); Alpacinche, *Devoto & Rial Alberti 2321* (SI); Capital, *Ulibarri 492*, *Arturi* (SI 26961); Route 38, 30 km. SW of Catamarca City, *B. S. Vuilleumier 1224* (GH, SI); Pilciao, *Vervoorst 4255* (TEX). LA RIOJA: Gral. Lavalle, Guandacol, 950 m. elev., *T. Meyer 4232* (UC), *Ruiz Leal 18858* (SI), *Herbst 1096* (SI); Chilecito, *T. Meyer 3508* (LIL, UC); Dept. Independencia, Guayapas, *Hayward & Legname 3155* (LIL); San Nicolás,

Ruta 79, *Ruiz Leal 16593* (SI). SAN JUAN: Desamparados, *Rodrigo 2922* (LP, SI); Quebrada de Gualcamayo, El Salto, *Ruiz Leal 18971*, Río de los Piojos, *Ruiz Leal 18870* (SI); Angaco Sud, *Tinto 2003* (SI); Caucete, *Volponi & Zardini 105* (LP, SI); Calingasta, *Covas 527* (SI); Valle Fértil, Río Tumanas, *Piccinini & Leguizamón 1789* (BAB, SI). MENDOZA: Lavalle, *Roig 5932, 5933* (SI), *Ruiz Leal 9805* (SI); Las Heras, Ramblón, *Semper 229* (NY); Punta de las Lajas, *Ruiz Leal 9786* (SI); Dept. Santa Rosa, La Dormida, *Ruiz Leal 9453* (SI). SAN LUIS: Dept. Junín, El Talita, *Burkart 13986* (SI); Alto Pencoso, *Bruch & Carette*, II 1914 (LP, NY, UC); Bajo de Velis, *Kurtz 8531* (NY); Dept. Junín, Merlo, *T. Meyer 13874* (SI); La Calera, *Burkart 10694*, Capital, *Anderson 1452* (SI); Luján, El Plumerillo, *Báez 15* (SI); Quines, *B. S. Vuilleumier 1013* (GH, SI). CÓRDOBA: Dept. Tulumba, *Sayago 2624*; Intihuasi, *Sayago 3666* (SI); Ischilín, Pajarito a Copacabana, *Sayago 3648, 3650* (CORD, SI); Cosquín, *Sayago 1416* (SI); Ascochinga, *Nicora 1303, Giardelli 956* (SI); La Calera, *J. H. Hunziker 2640, 2641* (SI); Dept. Sobremonte, La Majadilla, *Sayago 1692, 1684* (SI).

OBSERVATIONS. The specimens cited from Bolivia, *Schmidt 102* and *136*, have leaflets 3–4 cm. long × 3 mm. broad, which look like those of var. *catamarcana* var. nov., but the legumes are straight, 20 cm. long, compressed, yellow, 1.2 cm. broad. They may represent a variety, but owing to the great variability in this species, a thorough study *in situ* is necessary to decide the question. *Vargas 2041*, from Peru, is similar in foliage, but the legume is thicker, shorter, and submoniliform.

COMMON NAME. The common name of this form in Bolivia, according to Schmidt, is "Capesi."

Prosopis chilensis var. **riojana** Burkart, Darwiniana 9: 75. 1949.

A tree of the general habit of var. *chilensis*; spines geminate, 1–3.5 cm. long. Leaves unijugate; leaflets somewhat puberulous, linear-unicostate, 1.7–4.5 cm. long × 1.5–4 mm. broad, the distance on the rachis between pairs 5–12 mm. Legume nearly straight, submoniliform, 7–22 cm. long × 1 cm. broad × 5–8 mm. thick, with 7 to 15 subquadrate endocarp segments, straw-yellow or more or less tinged with violet, thicker. Argentina, La Rioja, near Jagüel, type: *Burkart 12355* (SI).

NEW MATERIAL EXAMINED. **Argentina.** LA RIOJA: Famatina, *G. Covas 1313* (LP, NY); Route 9 near Arauco, *B. S. Vuilleumier 1022* (GH, SI). CATAMARCA: Belén, *Sayago 1959, 1483* (SI); Dept. Tinogasta, El. Puesto, *J. Hunziker & O. Caso 4030* (BAB, SI); Quebrada de la Troya, 1700 m. elev., *J. Hunziker & O. Caso 4036* (SI); Andalgalá, *P. Joergensen 1340* (UC).

Prosopis chilensis var. **catamarcana** Burkart, var. nov.

Differt foliolis latioribus, 2–5 mm. latis et leguminibus annularibus, latis, carnosulis.

TYPUS VARIETATIS: Argentina, Prov. Catamarca, Dept. Belén, *Ulibarri 581*, fruct., 26 I 1974 (SI).

The variety *catamarcana* differs from the typical variety in having broader leaflets, 2–5 mm. broad; the foliage of the tree and its twigs are reddish when dry; venation in the leaflets is more visible and tends to be palmate, because of several basal nerves subparallel to the costa. The type specimen has no spines, according to the collector, but similar specimens from the same locality do have spines. Leaves are uni- or bijugate (mostly unijugate), ample. Leaflets are sometimes more than 4 cm. long and there are 7 to 19 pairs per pinna, distant on the rachis. The legume is typical, straw-colored, fleshy, sweet, semicircular to annular, sometimes S-shaped, with parallel margins, 7–8 cm. in diameter of its curvature, ca. 1.3–2 cm. broad, compressed, the endocarp segments rectangular, broader than long, up to 30, the seeds transverse.

OBSERVATIONS. This is a remarkably abundant tree in the Belén region of Catamarca, the area for which it is named.

COMMON NAMES. The same as for var. *chilensis* in Argentina.

MATERIAL EXAMINED. **Argentina.** SALTA: Molinos, 2000 m. elev., *Ruiz Leal 21310* (SI). CATAMARCA: Dept. Belén, Belén, La Banda, Quebrada de Belén or Campo de Londres, *Sayago 1482, 1484, 1487, 1494, 1583, 1910, 1961, 1964, 1965, 1970, 3506* (SI); Andalgalá, Cuesta de la Chilca, 1250 m. elev., *Parodi 14252* (GH); Catamarca, without further locality, *Devoto, Lambois, & Rial Alberti*, Herb. Forestal *641, 650* (SI); Belén, *Ulibarri 574, 581* (SI, typus varietatis); along Río Andalgalá, *Solbrig 4215* (GH, SI), *Joergensen 967* (MO). TUCUMÁN: Tafí, Amaicha al Infiernillo, *T. Meyer 12317* (MO). LA RIOJA: Capital, *Giacomelli 1–3, 15 XI 1927* (SI, LIL); Chilecito, *T. Meyer 3508* (GH, LIL); General Lamadrid, Villa Castelli, *T. Meyer 4073*, 1350 m. elev. (GH); General Lavalle, Guandacol, *T. Meyer 4232* (GH). CÓRDOBA: Dept. San Alberto, Los Cerrillos, *Báez 20* (SI). **South-West Africa.** Namibia, cultivated and subspontaneous, Forest Research Officer, Pretoria, nos. *8, 9*, and *19* (SI); Ovitoto, 17° 10′ E, 22° 5′ S, *Gibson 13*, common name "omukara kaka," var. dubious (MO).

USES. Important tree locally for shade, timber, fuel, and concentrated forage or food (owing to its sweet, pulpy fruits). The presence of unarmed trees midst the common spiny population opens the possibility of obtaining valuable lines for cultivation. Other aims for selection purposes must be taller trunks and a greater quantity and quality of legumes, which are much eaten (as sweets, "patay") or drunk (as "aloja"), and constitute a staple food for cattle in these arid regions. *Prosopis chilensis* is sometimes cultivated in Argentina and Chile and deserves more attention in reforestation programs. According to the results of preliminary trials, it is one of the fast-growing species under arid conditions in Mendoza, Argentina (F. Roig, unpublished data).

OBSERVATIONS. According to the chemical data on flavonoid distribution in *Prosopis* (Carman), *P. chilensis* has a different array of flavonoids than do the similar Argentine and North American species, except for *P. alba*, which has exactly the same ones.

35. **Prosopis juliflora** (Swartz) DC. Prodr. **2**: 447. 1825, Mém. Légumin. **12**: 431. 1825; Burkart, Darwiniana **4**: 103. *pl. 22*. 1940; Johnston, Brittonia **14**: 83. 1962; Svenson, Am. Jour. Bot. **33**: 451. *pl. 11, figs. 1, 4, 5*. 1946; Hubbard in Bailey, Stand. Cyclop. Hort. **5**: 2811. 1922.

Mimosa juliflora Swartz, Prodr. 85. 1788, Fl. Ind. Occ. **2**: 986. 1800 ("piliflora").
Acacia cumanensis Humboldt & Bonpland ex Willdenow, Sp. Pl. **4**(*2*): 1058. 1805.
Prosopis cumanensis (Humboldt & Bonpland ex Willdenow) H.B.K., Nov. Gen. Sp. Pl. **6**: 310. 1823; Kunth, Synop. Pl. Aequinoct. **4**: 33. 1825.
Neltuma juliflora (Swartz) Rafinesque, Sylva Telluriana 119. 1838; Britton & Rose, N. Am. Fl. **23**(*3*): 184. 1928; Johnston, Brittonia **14**: 83. 1962; Britton & Killip, Ann. New York Acad. Sci. **35**: 154. 1936.
Mimosa salinarum Vahl, Eclogae Americanae **3**: 35. 1807.
Prosopis bracteolata DC. Prodr. **2**: 447. 1825.
Prosopis dominguensis DC. Prodr. **2**: 447. 1825.
Algarobia juliflora (Swartz) Bentham ex Heynh., Nom. **2**: 18. 1840, according to Johnston, Brittonia **14**: 83. 1962.
Prosopis vidaliana A. Naves, Descripcion de la especie botánica *Prosopis vidaliana*, *fide* F. Villar, "*P. vidaliana*," 1–19. *pl. 1, 2*. 1877, according to Johnston, Brittonia **14**: 83. 1962.
Neltuma occidentalis Britton & Rose, N. Am. Fl. **23**(3): 185. 1928.
Neltuma bakeri Britton & Rose, *Ibid.*
Neltuma pallescens Britton & Rose, *Ibid.*

Tree 3–12 m. tall, sometimes shrubby with spreading branches; wood hard; branchlets cylindrical, green, more or less round- or flat-topped, somewhat spiny with persistent, green (sometimes glaucous or grayish, not reddish) foliage, glabrous or somewhat pubescent or ciliate on the leaflets; spines axillary, uninodal, divergent, paired, or solitary and paired on the same branches, sometimes absent, not on all branchlets, measuring 0.5–5 cm. long, being largest on strong, basal shoots. Leaves ample, glabrous or pubescent, 1–4-jugate, commonly 1–3-jugate; petiole plus rachis (when present) 0.5–7.5 cm. long; pinnae 3–11 cm. long; leaflets 6 to 29, generally 11 to 15 pairs per pinna, elliptic-oblong, glabrous or ciliate, rarely pubescent, approximate on the rachis or distant a little more than their own width, herbaceous to submembranous (not subcoriaceous as in more xerophilous species and therefore often corrugated or curved when dried), emarginate or obtuse, mucronulate, pinnate-reticulately nerved; leaflets 6–23 mm. long × 1.6–5.5 mm. wide. Racemes spiciform, cylindric, 7–15 cm. long; rachis puberulent; florets as usual, greenish-white, turning light yellow. Legume straight with incurved apex, sometimes falcate, straw-yellow to brown, compressed, linear with parallel margins, stipitate and acuminate, 8–29 cm. long × 9–17 mm. broad × 4–8 mm. thick; stipe to 2 cm. long; endocarp segments up to 25, rectangular to subquadrate, mostly broader than long; seeds oval, brown, transverse.

DISTRIBUTION. Northern South America (Venezuela, Colombia), Panama, Central America to Mexico and the Antillean Islands; the type specimen from Jamaica, but apparently from introduced material. A neotropical, coastal species. Introduced for cultivation in northern Brazil and other countries in Asia. In the Antilles it seems to be introduced. Ekman (Arkiv Bot. 23A (6): 29. 1930), describes its increase in Haiti, where it is considered a nuisance.

COMMON NAMES. Cashaw (Jamaica, *teste* Fawcett & Rendle); bayahonda, mezquite or cambrón (Santo Domingo, Puerto Rico); baron (Haiti, *teste* B. Simpson, 1973); bayahonde (Haiti; from French, "baie-à-ondes"); algarroba or mezquite (Mexico); mareño (Mexico, Sinaloa, *teste* González Ortega); catzimec (Maya, Yucatán, Guatemala, *teste* Standley & Steyermark); carbón (El Salvador, Standley, *in schedula*); espino ruco (Honduras, Molina, *in schedula*); acacia de Catarina (Nicaragua, *teste* Standley, 1922); aromo, mancacaballo (Panama); algarrobo, cují, cují negro (*teste* García Barriga & Forero González); trupillo, mancacaballo (Colombia, *teste* Britton & Killip, 1936); cují, yaque, cují yaque, yaque blanco, yaque negro, cují negro (Venezuela, *teste* H. Pittier); cují amarillo, maíz criollo (the legumes which fatten cattle) (Guarico, *teste* R. Montillo); algarrobo (Ecuador, *teste* Rimbach, *in schedula*); algaroba (Brazil, northeastern states); aroma (Philippine Islands, *teste* Standley, 1922).

The most generalized names are "algarrobo" in Spanish speaking countries and "mesquite" in the Mexican-Texan area, but both are collective names for *P. juliflora*, *P. laevigata*, *P. glandulosa*, etc. in the north, and *P. chilensis*, *P. alba*, *P. nigra*, and similar species in the south, where "mesquite" is unknown; the original Quechuan name, now nearly abandoned, was "tacu" or "taco." In Venezuela the names "cují" or "yaque," not known outside, are employed.

"Algarrobo" was orginally the carob tree, *Ceratonia siliqua* L. from the Mediterranean countries, and this name was transferred by the Spaniards to the American trees of the *Prosopis* sect. ALGAROBIA alliance because of the similarity in form and uses of the legumes. "Algarroba" is the fruit of the "algarrobo," but the name is sometimes used to distinguish between nearby species or varieties.

OBSERVATIONS. *Prosopis juliflora* is used here in its original, restricted, and certainly biological sense. It was reestablished by the writer (*op. cit.* 1940) and accepted by L. Benson (1941), M. C. Johnston (1962), and other modern authors against the incorrect, all-embracing, collective *P. juliflora* concept of Bentham (1875, 1876), which was maintained by Standley (1922, 1926) and Standley and Steyermark (Fl. Guatemala, 1946) despite difficulties in definition derived from a tremendous variability within the whole sect. ALGAROBIA species complex. Nobody can deny the existence of these difficulties, and perhaps in no other plant group is the insufficiency of common herbarium material more apparent. The sect. ALGAROBIA species are a challenge for the new, refined taxonomic

techniques of cytogenetical, ecological, biometric, and phytochemical nature elaborated by other authors.

For the traditional taxonomist remains the task of clarifying the synonymy and correctly applying the existing binomials. However, it is already certain that *Prosopis juliflora*, *P. chilensis*, *P. alba*, *P. nigra*, etc. are good species.

Chemical results obtained by Carman on the distribution of different flavonoids in species of sect. ALGAROBIA indicate a complete coincidence in flavonoid content in *Prosopis juliflora*, *P. glandulosa*, *P. laevigata*, and *P. velutina*, all North American species, and differences between them and eight other South American species. These results substantiate the integrity of these taxa as species.

NEW MATERIAL EXAMINED. **Mexico:** Sinaloa, Mazatlan, along the beach, *Rose, Standley, & Russell 13720* (NY, type of *Neltuma occidentalis*); Mazatlan, Santiago Ixciuntla, esteros, *Gonzáles Ortega 6154* (MEXU); Sinaloa, Altata, littoral, *H. S. Gentry 5420* (MO); Michoacán, Cayaco, *Nelson 6961* (NY, type of *Neltuma pallescens*); Nayarit, Tres Marías Isl., *Ferris 5580* (MO); Guerrero, Acapulco, *F. A. Barkley 14140* (MO), *Paray 3045*, Galeana, San Luis, *Hinton 10886* (MEXU, MO); Oaxaca, Tequisistlán, *M. Ulloa Sosa 26* (MEXU). **Guatemala:** San Marcos, Ocós, *Steyermark 37767* (US). **Cuba:** *León & Pierre 3763* (NY), *Shafer 1041* (NY). **Jamaica:** Kingston, *Britton & Hollick 1748* (NY), *A. S. Hitchcock*, Sept.–Nov. 1890 (MO). **Santo Domingo:** Los Matos, *H. von Schrenk 52* (MO); Monte Cristi, Moncion, *Valeur 943* (MO). **Haiti:** Source Matlas to Port au Prince, *B. Simpson 6038–1* (GH, SI). **Curaçao:** Willemstadt, *J. H. Humziker 4926* (SI); Ascension, *Britton & Shafer 3053* (NY). **Montserrat:** *Shafer*, 21 I 1907 (NY). **El Salvador:** *Standley 20531, 20788, 23232* (US). **Honduras:** *Standley 20739* (US), *Molina 5126* (US). **Nicaragua:** Managua, *Garnier A-667* (US); Tamagasta peninsula, *Maxon et al. 7333* (US); Aserraderos Island, *Baker 188, 2076* (MO, isotype of *Neltuma bakeri*). **Panama:** Bella Vista, *Standley 25391* (US), *P. H. Allen 824* (US); S Darién, La Palma, *Pittier 6616* (US); Isla del Rey, *Duke 9525* (US); Chiriquí Prov., Burica peninsula, *Busey 494* (MO); Darién, Patiño, *Duke 10511(3)* (MO); Los Santos, Chitre, *Tyson et al. 3017* (MO); Panama, without further locality, *Maxon & Valentine 6958* (US), *Macbride 2621* (US). **Colombia:** Dept. El Valle, Cauca Valley, N of Palmira, 1050 m. elev., *H. García Barriga 6348* (SI); Magdalena, Fonseca, *Haught 4062* (SI); Santa Marta, *Fosberg 22119* (NY), *H. H. Smith 40* (NY); Cartagena, *Schott*, 11 III 1838 (NY); Dept. Boyacá, Cord. Oriental, *Cuatrecasas & García B. 9835* (SI); Santa Marta, playas arenosas, *Giacometto, Gutierrez, & Barkley 18 C-015* (LIL); Dept. Atlántico, Puerto Colombia, *Killip & Smith 21073* (NY). **Venezuela:** Lara, Barquisimeto, *Killip 37077* (SI), *Tamayo 2625* (SI); Carabobo, Maracay a Valencia, *Burkart 16131* (SI); Lara, El Tocuyo, *Pittier 13096* (MO, NY); Falcón, Istmo de Médanos, *Torres, Tamayo, & Tamayo* (SI 26929); Maracaibo y Cumanacoa, *Mocquerys*, 1893–94 (NY, SI); Anzoátegui, La Ceiba, *Vera & Vásquez 3832* (SI); Sucre, Carupano a Guaca, *Vera & Vásquez 3835* (SI); N. Venezuela, Isla S. Carlos, *Curran & Hanan 783* (NY). **Ecuador:** Manabí, San Vicente, *Asplund 16596* (NY); Islas Galápagos, *W. von Hagen 63c, Schimpff 175* (NY). **Peru:** loc.(?), *Juana Infantes Vera 2110* (SI). **Brazil:** Ceará, Fortaleza, *Luti 4273* (SI); Paríba, Joao Pessoa, cultivated, *Ducke 2319* (SI); Rio Grande do Norte, cultivated, *G. de Azevedo 1.2* (SI); Mossoró, *Burkart 30326* (SI). **Africa. Senegal:** Dakar, cultivated, *Burkart 24502*, fruct., 10 IX 1963 (SI); Dakar, *Adam*

343 (MO); St. Louis, *Adam 27018* (MO). **Nigeria:** Bornu, Maiduguri, *Vjor, F. H. I. 21943* (MO). **Sudan:** Kharthum, subspontané, *Roberty 5355* (MO). **Asia. Iraq:** Abu Ghraib, saline soil near Tel-Akrakoof, *Abbas al Ani & Jawad 8820* (UC); Abu Ghraib, roadside, *Barkley & Abbas 71* (MO). **Kuwait:** *M. L. Grant 15635* (MO). **Vietnam:** Saigon, *King 5639* (US). **India:** Allahabad, *Panigrahi 5853* (MO). **Sri Lanka:** Ceylon, *R. G. Cooray* 69.121.701 R, on roadside (MO). **Philippines:** Luzón, Bataan, Lamao, *H. M. Curran*, Forest Bureau *15562* (NY); Bataán, along shore, *R. S. Williams 379* (NY, US); Manila, *Merrill 370, 1853* (GH, MO, NY); Oriental Mindoro Prov., *J. Vera Santos 5178* (US); Island of Basilan, *De Vore & Hoover 72* (US); Malate, *J. T. Rosaly* (MO 1017448); Luzón, Zapote, Rizal Province, *Mendoza*, Philippine Nat. Herb. *3840* (MO).

Prosopis juliflora var. **inermis** (H.B.K.) Burkart, comb. et stat. nov.

Prosopis inermis H.B.K., Nov. Gen. Sp. Pl. **6:** 307. 1825; DC. Prodr. **2:** 447. 1825; Svenson, Am. Jour. Bot. **33:** 451 (sub *P. juliflora*). *pl. 1, fig. 4.* 1946.

This variety differs from var. *juliflora* in its finely pubescent leaflets and its lack of spines. It seems abundant in the region of Guayaquil, Ecuador. From herbarium material, even when spines are lacking, it is not aways possible to distinguish it from the typical variety.

MATERIAL EXAMINED. **Ecuador:** Prov. Guayas, Guayaquil, *A. A. de Delgado 47, 56–58, 66* (MO, SI); Guayaquil, "common, dominant tree in savanna," *E. L. Little, Jr. 6560* (NY); Guayaquil, *Asplund 15225* (NY); Santa Cruz, *W. von Hagen 4* (NY), *Valverde 952* (MO).

Prosopis juliflora var. **horrida** (Kunth) Burkart, comb. et stat. nov.

Prosopis horrida Kunth, Mimoses et autres plantes légumineuses. 106. *pl. XXXIII.* 1822; H.B.K., Nov. Gen. Sp. Pl. **6:** 306. 1823; DC. Prodr. **2:** 446. 1825.

Spiny tree 3–8 m. tall, the spines sometimes rare, geminate, axillary, 1.5–7.5 cm. long; branchlets flexuous, grayish or black. Leaves bi- to quadrijugate; petiole plus rachis 2.5–7 cm. long; pinnae 6–10 cm. long; leaflets 10 to 15 pairs per pinna, elliptic, ovate to oblong, ca. 1.5 cm. long × 0.4 cm. broad, distant on the rachis, pubescent, pale, reticulate-nerved, obtuse. Racemes 9–12 cm. long; florets greenish-white. Legume straight or subfalcate, compressed, submoniliform, 18–24 cm. long × 1–1.2 cm. broad (including the stipe, 1.5–2 cm. long, and an acumen of 1.3 cm.), brown, glabrous except for scattered hairs along the margin; seeds numerous, to 26; joints rectangular, broader than long.

COMMON NAME. Algarrobo (northern Peru).

MATERIAL EXAMINED. **Peru:** Dept. Amazonas, Prov. Bagua, 500–600 m. elev., 5° 50′ S lat., entre Bagua Grande (near Jaen) y Chamaya, *Ferreyra 15646* (UC); Prov. Bagua, Bagua Grande, San Julián-hill, *Hutchison 1501* (NY); Dept. Piura, Pariñas Valley(?).

USES. *P. juliflora* is highly esteemed in several tropical countries as a valuable tree for shade, timber, and forage legumes. It is cultivated in

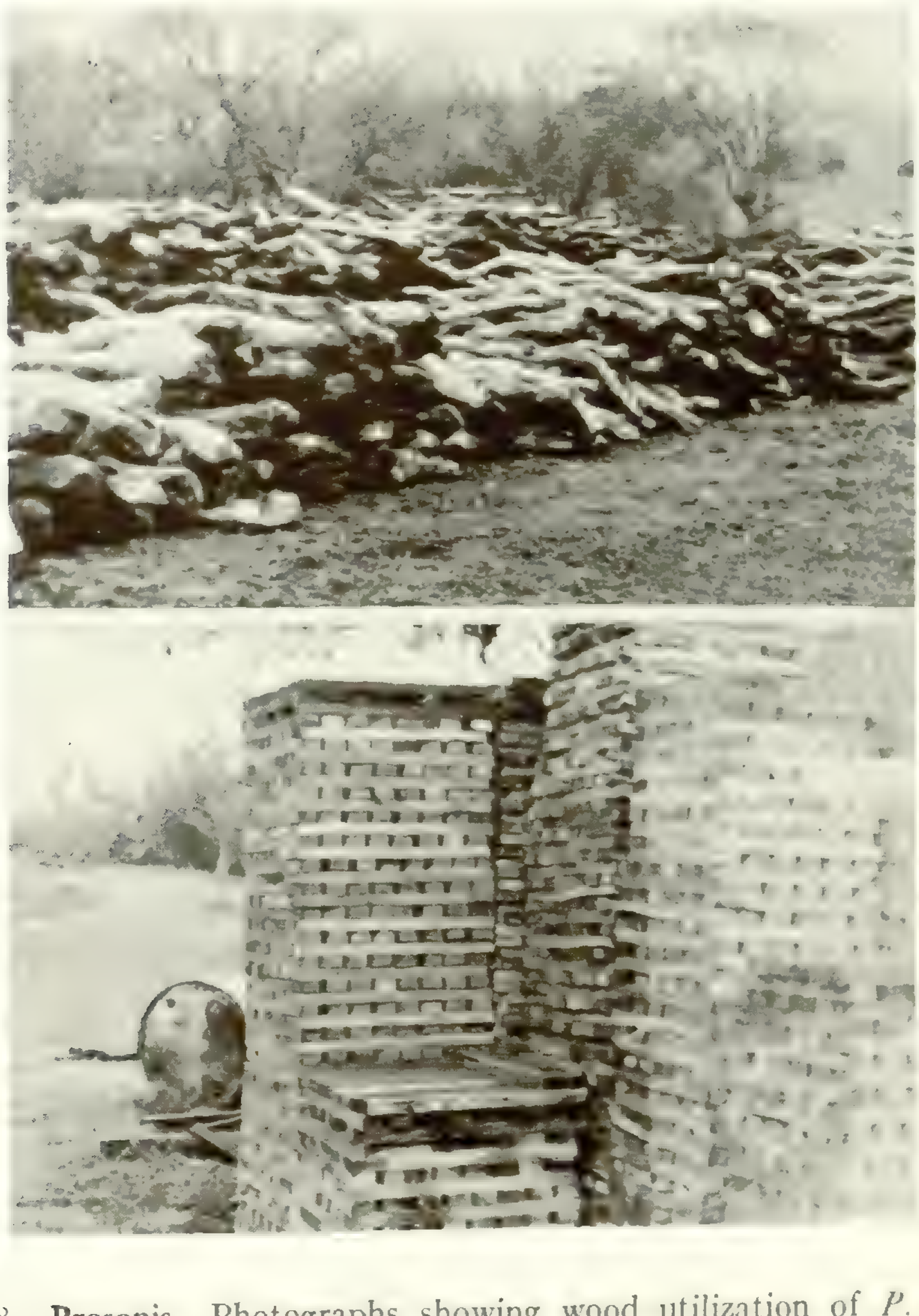

FIGURE 8. **Prosopis.** Photographs showing wood utilization of *P. nigra* and *P. affinis* from natural forests in western Uruguay. Above: Logs cut for fence-posts. Below: Timber cut for parquet floors. *Photos.* Marta Rolfo.

northeastern Brazil and in India. The shrubby forms, however, are sometimes a nuisance, as in Santo Domingo and Pakistan, where they are very aggressive invaders. *P. juliflora*, when in flower, is an excellent bee-pasture.

36. **Prosopis nigra** (Grisebach) Hieronymus. Plantae Diaphoricae. Bol. Acad. Nac. Córdoba **4**: 283. 1882; Burkart, Darwiniana **4**: 122. *fig. 15. tab. 21.* 1940.

Prosopis algarobilla Grisebach var. *nigra* Grisebach. Symb. Fl. Arg. in Abh. Kön. Ges. Wiss. Göttingen **24**: 118. 1879.

Prosopis dulcis Kunth var. *australis* Bentham. Jour. Bot. **4**: 350. 1842.

Round-topped tree 4–10 m. high (to 16 m. high *fide* Tortorelli): trunk with persistent, fissured, dark bark, to 50–80 cm. in diameter; heartwood dark brown; branches flexuous, the erect long shoots spiny, the

slender, downward-arching ultimate branchlets almost unarmed; spines, when present, axillary, geminate, 0.3–3.5 cm. long. Leaves uni- to trijugate, medium-sized, ample; petiole with rachis 4–6 cm. long; pinnae 5–10 cm. long; leaflets ca. 20 to 30 pairs per pinna, distant not more than their own width or approximate, oblong-elliptic, obtuse, pinninerved, glabrous, ciliolate, ca. 4–7 mm. long × 1.2 mm. broad. Spikelike racemes 7–9 cm. long, equalling the leaves; florets small, numerous, fragrant, greenish-white or yellow, nearly glabrous outside; petals 3 mm. long. Legumes straight or slightly subfalcate, thick, somewhat compressed, fleshy, submoniliform, 10–16 cm. long × 0.7–0.9 cm. broad, yellow, tinged with violet when ripe, edible, sweet; endocarp segments obliquely subquadrate, ca. 8 to 27; seeds ovate, 5–7.5 mm. long.

DISTRIBUTION. Southern Bolivia; Argentina; Paraguay; western Uruguay. Very important and abundant tree in the Gran Chaco formation from Córdoba and Buenos Aires provinces to the north; it thrives best on deep clay soils and tolerates alkali.

COMMON NAMES. Algarrobo negro; ibopé-hú (Guaraní); yura-tacu (Quechua).

NEW MATERIAL EXAMINED. **Argentina.** JUJUY: San Pedro a Urbana, *Killip 39632* (SI, US); San Pedro, Río Lavagin, *Eyerdam & Beetle*, Univ. Calif. Andes Exped. II *22534* (MO). SALTA: Coronel Moldes, *Bartlett 19711* (SI); Pichanal, *Carmelich, Devoto, & Rial*, Herb. Forestal *578* (SI). TUCUMÁN: Tapia, *Dawson & Calastremé 1811* (BAB, SI); Dept. Trancas, Vipos, *Schreiter 2253* (LIL, SI); Dept. Tafí, Banda, *Lillo 8730* (SI). CATAMARCA: El Ocho, *Parodi 14095* (SI); Catamarca, without further locality, *B. S. Vuilleumier 1124* (GH, SI). FORMOSA: Dept. Patiño, La Primavera, *Palacios et al. 328* (BAFC, SI); Ing. Juárez, *A. O. Bordón 74* (SI). Bart. de las Casas, 49 km. east, *Solbrig 4267* (GH, SI). CHACO: Zapallar, *T. Meyer 2199* (SI); Resistencia, Colonia Benítez y Saenz Peña, *Martínez et al.* (BAA *9506, 9526, 9628* (SI). SANTIAGO DEL ESTERO: Dept. Robles, Beltrán, *Maldonado 416* (LP, NY, SI); Dept. Choya, Frías, *Sayago 2639* (SI); Ruta 64 de Capital a Cerrillos, *Burkart 20348* (SI); Dept. Moreno, Quimilí, *Krapovickas & Cristóbal 20450* (SI). CÓRDOBA: Dept. San Justo, surroundings of Mar Chiquita, *Sayago 3631, 3634, 3638, 3639* (SI); Río Primero, La Posta, *Sayago 1711* (SI); Córdoba a Calera, *A. T. Humziker 8123* (SI); Dept. Capital, *Sayago 2014, 2018* (SI); Dept. Sobremonte, *Sayago 1696* (SI); Capital, *Rodrigo 277* (LP, SI); Dept. Colón, Núñez del Prado, *Sayago 1298, 1299* (SI); Pozo del Tigre, *Sayago 1290* (SI). SAN LUIS: Capital, *Andersen 658* (SI). SANTA FE: Dept. Gral. Obligado, Lanteri, *Burkart 5927* (SI). CORRIENTES: Paso de los Libres, *Correa et al. 5230* (SI); Mburucuyá, Santa María, *Pedersen 3754* (MO, NY, SI, UC); San Roque, *Ibarrola 2952* (UC). ENTRE RÍOS: Paraná, *J. R. Báez* (SI 17959), *Burkart et al. 23701* (SI); Nogoyá, *Burkart 10516*, Diamante, *Burkart 22186* (SI). BUENOS AIRES: Partido de Zárate, Las Palmas, *Boelcke 5139* (SI).

USES. *Prosopis nigra* is a very important and valuable timber tree, much used for furniture, barrels, tanning, firewood, forage and food (sweet fruits), bee-pasture, shade, and ornament in dry climates. It reproduces

FIGURE 9. **Prosopis.** Photograph of *P. nigra*, a partial view of an historic specimen growing in the Quebrada de Humahuaca, Purmamarca, Jujuy, Argentina. According to Burkart the age of this tree has been calculated to be at least 400 years.

FIGURE 10. **Prosopis.** Left: Photograph of trunk of a large tree of *P. nigra* in western Uruguay. Right: Wood pile of *P. nigra* prepared for charcoal. *Photos.* Marta Rolfo.

freely and is seldom cultivated, but it is worthy of attention and the selection of the best growth types. Nowhere is it considered an invader.

OBSERVATIONS. *Prosopis nigra* is a somewhat variable species and its limits are not always clear. This fact is probably due to its hybridization with *P. alba* or *P. flexuosa* on the western boundaries of its area.

Type specimens of *Prosopis nigra* are *Hieronymus 486* and *905* (GOET), as stated in my paper of 1940 (*pl. 21*). Photographs 1458 and 1466 of the Field Museum series represent *P. nigra* (not *P. algarobilla* or *P. nandubey*).

Two variants, *Prosopis nigra* var. *ragonesei* and var. *longispina*, merit taxonomic recognition.

Prosopis nigra (Grisebach) Hieronymus var. **ragonesei** Burkart, Darwiniana 7: 518. 1947; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 1. 127. *fig. 16*. 1943, ed. 2. 127 (*fig. 19*), 132. 1952.

Tree unarmed or with very small, axillary spines, of the general habit of var. *nigra*, but characterized by very small, more ovate leaflets 1.5–3.2 mm. long, the legume compressed-moniliform, straight and less sweet;

the heartwood yellow, less durable. The picture cited in *Las Leguminosas Argentinas, silvestres y cultivadas* was drawn from the type specimen.

DISTRIBUTION. Argentina (Prov. Santa Fe, Dept. San Justo, Dept. Vera, etc.).

COMMON NAME. Algarrobo amarillo.

MATERIAL EXAMINED. **Argentina.** SANTA FE: Videla, *A. E. Ragonese*, Herb. Inst. S. Fe *2078* (SI, type); Dept. Vera, arr. del Toba, Herb. Inst. S. Fe *2420* (SI); Vera, *Burkart 5933* (SI).

Prosopis nigra (Grisebach) Hieronymus var. **longispina** Burkart, var. nov.

Differt a var. *nigra* imprimis spinis longis rectis, subulatis tenuibus, haud supra basin dilatatis, circa 0.5–10 cm. longis; arbor valde armatus, ramulis pendulis habitu et alteris characteribus cum var. *nigra* congruit.

TYPUS VARIETATIS: Argentina, Prov. Corrientes, Dept. Capital, *Pedersen 2808*, fl., 23 IX 1954, ripe fr., 15 II 1955 (SI).

This new variety differs from var. *nigra* in its spiniferous branchlets, the axillary spines being geminate, straight, 0.5–10 cm. long × at most 3 mm. in diameter, without suprabasal enlargement (such as that seen in *Prosopis elata*) and much more slender than in *Prosopis pugionata* (which differs moreover by leaflets distant on the rachis). All other characters of the tree are those of var. *nigra*, including the pendulous growth of the slender branchlets, which produces a globose treetop.

The collector of the type specimen, Mr. Pedersen, informs me that this spiny variety is locally common, as is var. *nigra* (nearly spineless or with very small spines), so that natural crossing must be possible.

DISTRIBUTION. Argentina (Prov. Corrientes, Eastern Chaco).

COMMON NAME. Algarrobillo (a diminutive of algarrobo, the common Spanish name for all of the arborescent species of sect. ALGAROBIA).

MATERIAL EXAMINED. **Argentina.** CORRIENTES: Capital, *Pedersen 2808* (SI, isotype; holotype, C). CHACO: Colonia Benítez, not far from Resistencia, *Schulz 1356* (SI).

37. **Prosopis caldenia** Burkart, Darwiniana 3(2): 111. *pl. 1.* 1939, 3(1): *pl. 6* ut "Prosopis" cfr. "fruticosa" Meyen. 1937, 4: 110. 1940; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. 132. *pl. 2, fig. 1.* 1952.

Tree with deciduous foliage, medium-sized, round-topped, 4–12 m. high and 15 m. in diameter at top; trunk short, 20–80 cm. in diameter, in old specimens to 1.5 m. in diameter (trees of more than 100 years); bark persistent, fissured, dark; branchlets flexuous, knotty; spines axillary, geminate, uninodal, divergent, not more than 0.5–2.5 cm. long. Leaves small, light, glabrous or puberulous (rachis, leaflet-margins), uni- to

quadrijugate (on long shoots mostly bi- to quadri-jugate, on brachyblasts or axillary fascicles uni- to bijugate); petiole plus rachis 4–25 mm. long; pinnae 2–5.5 cm. long; leaflets ca. 20 to 33 pairs per pinna, linear-oblong, small, enervate or unicostate, obtuse, approximate, glabrous, ciliolate, 2.7–5.4 mm. long × 0.2–1.1 mm. broad. Racemes spikelike, longer than the leaves; peduncle plus rachis 3.5–9 cm. long; pedicels 0.7–1 mm. long; florets greenish-white to yellowish; calyx (1 mm. long) and corolla glabrous outside, the petals 2.5–3 mm. long, villous at the apex; stamens 6 mm. long; ovary stipitate, villous. Legume compressed-linear, falcate, in S- or C-shape or in 1–3 very lax and open spirals 10–20 cm. long × 5–13 mm. broad, stipitate and acuminate (acumen or rostrum 0.5–1.7 cm. long); margins parallel, straw-yellow, violet-tinged; endocarp segments quadrate or transversely rectangular, in one row, up to 35; seeds ovate, 5–7.5 mm. long.

DISTRIBUTION. Endemic to south-central Argentina, forming open unispecific, semixerophytic woods or forests in the plains of the western Pampas region (Prov. La Pampa, San Luis, southern Córdoba, etc.) and very sporadic elsewhere; asociated with *Stipa*-dominated grassland and few shrubs in a continental climate of warm, dry summers and cold winters (rarely with snow), most frequently between 35° and 38° S. latitude, and 65° W. longitude, the rainfall 420–630 mm. mean per year, the mean annual temperature 15–16.5° C. *Prosopis caldenia* does not tolerate saline soils, but rather soils with a good deal of sand in their composition.

COMMON NAME. Calden.

MATERIAL EXAMINED. **Argentina.** CÓRDOBA: V. Dolores, Ruta 146, *Báez 12* (SI); Rio Cuarto, *A. T. Hunziker 9369* (CORD, SI); Dept. Gral. Roca, Rio Quinto, *Sayago 730* (SI). SAN LUIS: Coronel Pringles, *A. I. Pastore 2070, 2071* (GH); Dept. Junín, Santa Rosa, *Báez 1–3* (SI); Capital, *Burkart 10671* (SI), *Anderson 1486* (SI); Villa Mercedes, *Nicora 4233* (SI). MENDOZA: Dept. La Paz, various places, *Ruiz Leal 9066, 9448, 9507, 9591* (SI); Dept. Santa Rosa, Campo La Dormida, *Ruiz Leal 9867*, General Alvear, *Ruiz Leal 21761* (SI). LA PAMPA: Dept. Rancul, La Maruja, *Burkart 9959* (SI); Dept. Leventue, *B. Vuilleumier 1002–3, 1004–3, 1005–10* (BAA, SI); Catriló, Uriburu, *Fortuna 20* (GH, UC); Santa Rosa a Victorica, *Cabrera 4353* (GH); Sta. Rosa, *Venturi 452* (GH); Realicó, *A. T. Hunziker 9393* (SI); Dept. Utracán, Cuchillo-Có a Epupel, *Solbrig 172* (SI); Dept. Hucal, Villa Alba, *A. T. Hunziker 4240* (SP); Bernasconi, *Bartlett 20006* (GH, SI, US); Rancul a Chamico, *Cabrera & Crisci 19101* (LP, SI); General Acha, *Burkart 15995* (SI); Km. 358, *B. S. Vuilleumier 1001*; Loventuel, *Vuilleumier 1002, 1102*; Telén a Colonia La Pastoril, *B. S. Vuilleumier 1105* (GH, SI); Toay District, Santa Rosa, *Conrad 2370* (MO). BUENOS AIRES: Bahía Blanca a Médanos, *Burkart 25628* (SI); Villarino, *Boelcke et al. 11780* (SI), *Cabrera & Fabris 16438* (LP, SI), *Alsina, Cabrera, & Fabris 14799* (LP, SI); General Villegas, *Schulz 5784* (LIL, NY). RÍO NEGRO: Dept. Pichi Mahuida, Río Colorado, *Ragonese* (SI *26957*).

USES. *Prosopis caldenia*, the "calden," is the only large tree in its range and forms characteristic forests commonly associated with grass-

land and scrub. It furnishes valuable timber, but this is inferior to that of *P. alba* and other "algarrobos"; nevertheless, it is considered good for furniture. The legumes serve as concentrated forage for cattle. Wild life, such as foxes (Dusicyon), guanacos, ostriches, and naturalized wild boars, feed on them.

When the "caldenales" are cleared for agriculture and later abandoned because of the frequent droughts, abundant germination occurs, and in a few years spiny, impenetrable thickets are formed, known locally as "fachinales." They provide an excellent refuge for wild life, but are for years useless to the rancher.

Literature on *Prosopis caldenia*: J. V. Monticelli, Lilloa 3: 348. 1938 (sub *Prosopis calden*, nomen nudum); Koutché & Carmelich, Estudio forestal del Caldén, Bol. Ministr. Agr. Nac. 37(1–4): 1–22. *illustr.* Buenos Aires, 1936 (sub *P. algarobilla* auct., non Grisebach); J. L. Alfonso, in Anal. Soc. Ci. Arg. 159: 37–57. Buenos Aires, 1955; J. C. Lassalle, Política forestal del Caldén, Ingeniería Agronóm. 15(4): 5–15. Buenos Aires, 1957, Rev. Forestal Arg. 10: 15–19. 1966, *Ibid.* 6: 44–50. Buenos Aires, 1962; L. A. Tortorelli, Maderas y Bosques Argentinos 399, 403. Buenos Aires, 1956.

This species grows in a climate with hot summers and cold winters (with snow when not too dry), so that the wood forms clear growth-rings and has been successfully used in dendrochronology (Krebs, C. & G. Fischer, El pluviómetro secular, Circ. Sec. Prop. & Inf. Ministr. Agr. 847: 1–24. Buenos Aires, 1931).

38. **Prosopis laevigata** (Humboldt & Bonpland ex Willdenow) M. C. Johnston, Brittonia 14: 78. 1962; Isely, Madroño 21: 289, 294. 1972.

Acacia laevigata Humboldt & Bonpland ex Willdenow, Sp. Pl. 4(2): 1059. 1805.
Mimosa laevigata (Willdenow) Poiret in Lamarck, Encycl. Méth. Bot. Suppl. 1: 65. 1810.
Neltuma laevigata (Willdenow) Britton & Rose, N. Am. Fl. 23(3): 187. 1928.
Prosopis dulcis Kunth, Mimoses et autres plantes légumineuses. 110. *pl. 34.* 1822; DC. Prodr. 2: 447. 1825; Humboldt, Bonpland. & Kunth, Nov. Gen. Sp. 6: 307. 1823.
Algarobia dulcis (Kunth) Bentham, Plantae Hartwegianae 13. 1839.
Neltuma attenuata Britton & Rose, N. Am. Fl. 23(3): 185. 1928.
Neltuma michoacana Britton & Rose, N. Am. Fl. 23(3): 187. 1928.

Tree, becoming large with age, spiny, to 6–7 m. tall, sometimes a shrub of 3 m.; twigs and leaves glabrous; spines axillary, geminate, 0.5–2.5 cm. long. Leaves uni- to bijugate; petiole (plus rachis when extant) 0.3–2.5 cm. long; pinnae 2.5–12 cm. long. Leaflets numerous, approximate (interval on the rachis smaller than their width), 15 to 44, mostly 20 to 30 pairs per pinna (in topotype material, 15 to 20 pairs), linear-oblong, obtuse, glabrous or scarcely ciliolate on margin, 2.5–15 mm. (mostly 5–10

mm.) long × 1.1–3 mm. broad (2 to 7 times as long as broad (topotype material 3 to 4 times) according to Johnston, 1962), subcoriaceous (flat after desiccation, not corrugated as they commonly are in *P. juliflora*), pallid greenish to grayish, strongly pinnate-veined beneath. Racemes spiciform, 4–10 cm. long, multiflorous; flowers greenish-white; calyx 1 mm.; petals 3–4 mm. long. Legume 9–17 cm. long × 0.7–1.4 cm. broad, linear, glabrous, straight or slightly curved, submoniliform, yellow or violet-sprinkled, compressed; transection rectangular or rounded at maturity; margins undulate; segments rounded-subquadrate, shorter than broad; stipe 0.2–1 cm. long; acumen 0.3–1 cm. long; epicarp veined, crustaceous, yellow or violet-tinged; seeds longitudinal.

DISTRIBUTION. Mexico, especially the central plateau and hillsides (cf. M. C. Johnston, Brittonia **14**: 73. *fig. 1.* 1962); U.S.A., rare in Nueces Co., Texas.

COMMON NAME. Mezquite (from the Nahuatl "mezkitl," masc. noun), applied to this and related species in Mexico and the United States.

MATERIAL EXAMINED. **Mexico:** Tamaulipas, Tampico, *E. Palmer 229* (NY); San Luis Potosi, *Schaffner 593* (NY), *Roe et al. 66* (NY); Zacatecas, Jalpa, *Mahler 5800* (NY); Jalisco, Juanacatlán, 1600 m. elev., *Rzedowski 16339* (US); Hidalgo, Actopan, *King 4197, 4203, 4205* (NY), *Pringle 8350* (NY); Michoacán, Punguato, *Arsène 8297* (GH; NY; MO, type of *Neltuma michoacana*); Morelia *G. Arsène 8447* (GH, isotype of *Neltuma attenuata;* MO, NY); Puebla, Tehuacán a Puebla, *Gentry, Barclay, & Argüelles 20212* (US); Tehuacán area, above Calipán, 1000–1800 m. elev., *C. E. Smith et al. 3746* (US); Guerrero, Coyuca, *Hinton 5471* (NY); Valle de Oaxaca, *Conzatti 5158* (SI); Oaxaca, cerros de Cuicallán, 650 m. elev., *Conzatti 3423* (SI); Oaxaca Valley, *C. L. Smith 341* (NY); Puebla, Tehuacán, *Paray 294*, Michoacán, San José, *Rzedowski 16653*, Hildalgo, Tasquillo, *González Q. 2634* (ENCB); Guanajuato, Silao, *Crutchfield & Johnston 5941-AB* (TEX); Aguascalientes, *C. D. Johnson 50-68* (MO).

USES. Esteemed as a shade tree; cultivated in the central depression of Chiapas (according to Johnston, 1962, p. 79); legumes edible and of value as fodder.

Prosopis laevigata var. **andicola** Burkart, var. nov.

Differt imprimis ramis spinisque validioribus, ramulis valde flexuosis spinis usque ad 4–9 cm. longis × 5–6 mm. diametro, foliolis majoribus, legumine crassiori. Frutices 1–3 m. alti, rarius arborei, folia unijuga, foliola ca. 24 paria per pinna, racemi 10 cm. longi, legumina subfalcata linearia 15–20 cm. longa × 1.2–1.4 cm. lata compressa multiseminata.

TYPUS VARIETATIS: Peru, Cuzco, Prov. Calca, Hacienda Urco, *César Vargas C. 709*, floribus fructibusque ornatus, Januar, 1938 (SI).

Shrubs of 1–3 m. or more, rarely trees to 5–8 m. tall, glabrous; twigs strong, very flexuous; spines geminate, axillary, the most developed 4–9 cm. long × 5–6 mm. broad at base. Leaves unijugate; petiole 0.2–3 cm.

FIGURE 11. **Prosopis.** Flowering specimen of *P. laevigata* var. *andicola* from Cerro de Araní, Cochabamba, Bolivia (*Cardenas 3647*) (GH).

long; pinnae 5–9 cm. long, with ca. 16 to 24 pairs of leaflets, these subcoriaceous, linear-oblong, obtuse to subacute, reticulate-veined, 5–12 mm. long × 1.5–2.2 mm. broad, approximate, nearly touching or less distant than their own width. Racemes 6–10 cm. long, the rachis puberulous; florets glabrous outside. Legume subfalcate, 7–20 cm. long × 1.1–1.4 cm. broad, compressed; margins shallowly undulate to nearly parallel; transection rectangular; exocarp brown-violet.

COMMON NAMES. Algarrobo (Spanish); thako (Quechua).

OBSERVATIONS. A montane type of a variable, subxerophilous, Mexican species, at medium elevations (1900–2900 m.). Formerly sometimes cited as *Prosopis dulcis* Kunth or *P. juliflora* (Sw.) DC. DISTRIBUTION: from southern Peru through the Bolivian Andes to the extreme northwestern corner of Argentina (Jujuy).

MATERIAL EXAMINED. **Peru:** Cuzco, Calca, Hacienda Urco, *C. Vargas C. 709* (SI, type); Arequipa, Tiabaya, rocky slopes 2000–2100 m. elev., *Pennell 13062*, with mature legumes, 8 IV 1925 (GH, NY). **Bolivia:** Cochabamba, Cerro de Aranî, 2600 m. elev., *Martin Cárdenas 3647*, flowering, III 1944 (GH, LIL, SI); Cochabamba, 2600 m. elev., *O. Kuntze*, III 1892, sub. *P. juliflora* (NY); Tarija, Prov. Cercado Tarija, 1900 m. elev., *T. Meyer 17965*, fruct., I 1953 (LIL, SI); Sorata, Prov. Larecaja, San Pedro, 2650 m. elev., *Mandon 758* (NY); Tarija, Pinos, *Fiebrig 2492* (SI); Cotaña am Illimani, *Buchtien 280* (NY). **Argentina:** Prov. Jujuy, Tilcara, *Krapovickas & Cristóbal 17593*, fl. and fruct., 8 I 1971 (SI); Huacalera, quebrada a 2700 m. s.m., *Cabrera 12076* (SI).

39. **Prosopis flexuosa** DC. Prodr. 2: 447. 1825; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. 131. 1952; Burkart, Leguminosae in Cabrera, Fl. Prov. Buenos Aires 3: 429. 1967; Clos in Gay, Fl. Chilena 2: 248. 1846.

Acacia flexuosa Lagasca, Gen. Sp. 16. 1816 (non *A. flexuosa* Humboldt & Bonpland ex Willdenow, Sp. Pl. 4: 1082. 1805).

Prosopis juliflora (Sw.) DC. forma *arborea* L. Hauman, Anal. Mus. Nac. Buenos Aires 24: 391. 1913.

Prosopis fruticosa F. J. F. Meyen, Reise um die Erde . . . 1830–1832 1: 376, in obs. Berlin. 1834; Vogel, Leguminosae in Meyenii Obs. Bot., Nova Acta Acad. Leop.-Carol. Suppl. 2: 44. 1843.

Trees or large, erect, polypodial shrubs, 3–10 m. tall; hemispherical top with ultimate branchlets bent down, pendulous, flexuous and knotty in age; spines axillary, geminate, commonly small or absent but sometimes, on strong shoots, robust and to 3–4 cm. long; foliage light, deciduous, ample. Leaves uni- to trijugate, glabrous or scarcely puberulous; petiole (plus rachis when extant) 0.6–7.5 cm. long; pinnae 5–13 cm. long; leaflets linear, opposite, distant and medium-sized, 12 to 29 pairs per pinna, the distance between them on the rachis more than their own width or mostly several times larger, obtuse to subacute, cuneate or parallel-margined, 4–15 mm. long × 1–2 mm. broad, subcoriaceous, uninerved below or secondary veins slightly visible. Racemes spiciform, 4–14 cm. long, with ca. 200 flowers each, densiflorous and similar to those of related species, as are the florets. Legume nearly straight or subfalcate, 5–28 cm. long × 0.7–1.2 cm. broad, thick, subcompressed, submoniliform (margins undulate), straw-yellow, tinged with violet to nearly black-violet; joints subquadrate-rotund, hard, closed; pulp sweet, more or less developed.

DISTRIBUTION. Northern Chile (Atacama, Coquimbo) and Argentina, very common in the arid regions of the west, from Tucumán and Catamarca, through La Rioja, western Córdoba, San Juan, San Luis, and Mendoza, to La Pampa, Río Negro, and western Buenos Aires provinces. This area characterizes the species as a typical "Monte" tree, of much importance in the formation of open-desert forests along temporary rivers, with *Larrea* div. sp. (Zygophyllaceae), Cactaceae, etc. The species is sometimes found at elevations of 2200 m. in valleys of the Andes.

COMMON NAMES. Algarrobo, algarrobo dulce, algarrobo negro, algarrobo amarillo, panta negro, árbol negro, lámar, lámaro (Argentina); algarroba (Chile).

OBSERVATIONS. Chemical data on flavonoid content, obtained by Carman, indicate a close affinity of *Prosopis flexuosa* with other Argentine species of the same section (sect. ALGAROBIA), e.g., *P. caldenia* and *P. nigra*, but strong differences from the North American species *P. juliflora* and its allies.

SELECTED SPECIMENS EXAMINED. **Chile:** Dept. Atacama, Copiapó, *Werdermann 455* (GH, LIL, SI). *C. Jiles 2076* (LIL); Atacama, *Morong 1206*, Sept.–Oct. 1890 (NY); Copiapó, *Cabrera 11380* (SI); Dept. Coquimbo, Dept. Elqui, Casablanca, *R. Wagenknecht*, IX 1940, Univ. Calif. Andes Exped. *18564* (UC); Dept. Coquimbo, *Looser 4332, 4336, 4337, 4482* (SI). **Argentina.** TUCUMÁN: Dept. Tafí, Colalao del Valle, *Ruiz Leal 12319* (SI). CATAMARCA: Santa María, *Schulz 7328* (SI); Belén, *Sayago 1480, 1481, 1506, 1565, 1567, 1585, 1632* (SI); Andalgalá 1200 m. elev., *Parodi 14253* (SI); Andalgalá, Route 1, *Solbrig 4219* (GH, SI); Belén, *Ulibarri 583, 589* (SI); Ambato, *B. Vuilleumier 1024–1* (SI); Andalgalá, *Joergensen 1340* (SI); Capital, Choya, *Castillón* (LIL 54659, GH). LA RIOJA: Tello, *Ruiz Leal 17199* (SI); Ileal cerca de Olta, *Castellanos*, II 1940 (BA 33666, SI); Gral. Sarmiento, Cienaguita, Río Bonete, *J. H. Hunziker 2230* (MO); Gob. Gordillo, *Ruiz Leal 16500, 16584, 17141* (SI); R. Vera Peñaloza, *D. L. Anderson 1530* (SI); Villa Unión to Patquía, *B. Vuilleumier 2026–1–3* (TEX); Jagüel a Cortaderas, *Lorentz & Hieronymus 270* (CORD); Chilecito, *Covas 1333* (NY); Gral. Lavalle, Villa Unión, *T. Meyer 4145* (UC). SAN JUAN: Loc. (?), *A. P. Rodrigo* det. (LP, SI); San Agustín del Valle Fértil, *Bartlett 19539* (SI). MENDOZA: Dept. Lavalle, *Ruiz Leal 13838, 13842, 14522, 14533, 14539* (SI); La Paz, *Ruiz Leal 23357* (SI); Las Heras, Jocolí, *Semper 149* (NY); Ñacuñan Reservation, *Roig 5396* (SI); General Alvear, *Ruiz Leal 21744* (SI). SAN LUIS: Dept. Pringles, Trapiche, *Roig 5648, 5666* (SI); Capital, San Gerónimo, *Burkart 10701* (SI), *Anderson 1456* (SI); Margen Río Quinto al NW de Fraga, *F. Pastore 2072* (GH); Bajode de Velis, *Kurtz 8489* (NY), *Kurtz 8450* (CORD). CÓRDOBA: San Javier, *Sayago 1428, 1431, 1453* (SI); Villa Dolores, *Burkart 7578*; Villa Dolores a Chancaní, *A. T. Hunziker 11512, 11519* (SI). LA PAMPA: Parque Luro entre Santa Rosa y General Acha, *Burkart 20467*, *Boelcke & Nicora 7949* (SI); Epupel, *Solbrig 178* (SI); Santa Isabel, *Cabrera 4386* (LP, SI); between Telén and Colonia La Pastoril, *B. S. Vuilleumier 1205* (GH, SI). RÍO NEGRO: De Garay a Choele-Choel, *Burkart 1588.3* (SI). BUENOS AIRES: Adolfo Alsina, *Cabrera & Fabris 14808*, Carhué, *Burkart 4755*, Guaminí, *Nicora 4175*, Villarino, *Cabrera & Fabris 16429* (SI).

Prosopis flexuosa forma **subinermis** Burkart, forma nova.

Arbor spinis fere totus destitutus.

Trees totally or nearly unarmed. Bark (in the type) glaucous-reddish, smooth. Leaflets distant, 5–13 mm. long.

MATERIAL EXAMINED. **Argentina.** TUCUMÁN: Tafí, Amaicha del Valle, *Burkart 22058* (NY, SI). SAN JUAN: Calingasta a Barreal, entre La Isla y Sorocayense, *J. H. Hunziker 6451* (SI, typus formae). BUENOS AIRES: San Isidro, barranca del Río de la Plata en Acassuso, *Burkart 12735, 25587, 28239* (SI).

OBSERVATIONS. *Prosopis flexuosa* DC. is a variable species but well delimited. From *P. chilensis* it differs in its shorter leaflets, the smaller size of the tree, and the submoniliform legume; from *P. nigra* it differs in its longer and more distant leaflets; from *P. alba* it varies in its obtuse, more distant and less numerous leaflets and the submoniliform legume; and from *P. alpataco* it varies mainly in its tree habit.

Prosopis flexuosa shows affinity with the vicarious *P. laevigata*, *P. velutina*, and *P. glandulosa* in western North America. Again the main differences are found in the leaflets, which in the latter three species are more approximate on the rachis, or pubescent, or larger, respectively, than in *P. flexuosa*, as well as in legume differences and variation in other minor characters.

Nomenclaturally *Prosopis flexuosa* has to be considered as a species founded by De Candolle and not as a combination based on Lagasca's *Acacia flexuosa*, which, in spite of being based on the same plant, was a later homonym preoccupied by *Acacia flexuosa* Humboldt & Bonpland ex Willdenow.

Prosopis fruticosa Meyen is included here in the synonymy of *P. flexuosa* DC. for the first time. It is impossible to find any significant difference between them. Topotype material of Meyen's species (from Copiapó, Chile) has been examined.

USES. As in similar species, an important tree for shade, timber, firewood, food, and forage in semidesert conditions such as the Monte formation, where rainfall ranges from 50 mm. to 100 mm. per year.

40. Prosopis glandulosa Torrey, Ann. Lyceum Nat. Hist. New York **2**: 192. *pl. 2*. 1827; Cocks, Leguminosae of Louisiana, Bull. Nat. Hist. Surv. Louisiana State Mus. 1: 1–26. *illustr*. New Orleans. 1910; Johnston, Brittonia **14**: 82. 1962; Isely, Madroño **21**: 290. 1972.

Algarobia glandulosa (Torrey) Cooper, "The Mezquite Bean" in The Scientific Press, San Francisco, Calif. 4 Nov. 1871.

Prosopis juliflora (Swartz) DC. var. *glandulosa* (Torrey) Cockerell, Bull. Agr. Exp. Sta. New Mexico **15**: 58. 1895; Jepson, Flora of California **2**: 239. 1936; Benson, Am. Jour. Bot. **28**: 752. 1941; Standley, Contr. U. S. Natl. Herb. **23**(2): 353. 1922.

Prosopis juliflora (Swartz) DC. var. *constricta* Sargent, Trees & Shrubs **2**: 249. *pl. 193*. 1913.

Prosopis chilensis (Molina) Stuntz var. *glandulosa* (Torrey) Standley, Contr. U. S. Natl. Herb. **23**(5): 1658. 1926.

Neltuma glandulosa (Torrey) Britton & Rose, N. Am. Fl. **23**(3): 186. 1928.

Neltuma constricta (Sargent) Britton & Rose, *Ibid.*

Neltuma neomexicana Britton, *Ibid. teste* Isely, Madroño **21**: 292. 1972; Benson, Am. Jour. Bot. **28**: 752. 1941.

ILLUSTRATIONS. C. S. Sargent, Silva N. Am. **3**: 101 (text, in part). *tab 136, 137*. New York. 1947. (sub *P. juliflora*); Svenson, Am. Jour. Bot. **33**: 453. *pl. 11, fig. 2*. 1946.

Tall shrub or tree of 3–9 m.; foliage deciduous; spines axillary, uninodal, 1–4.5 cm. long, mostly solitary, sometimes very few, or solitary and geminate alternately on different nodes of the same twig. Leaves glabrous, uni- or bijugate; petiole (with rachis when extant) 2–15 cm. long; pinnae 6–17 cm. long; leaflets 6 to 17 pairs, ca. 7–18 mm. distant on the rachis, linear or oblong, obtuse, glabrous, subcoriaceous, prominently veined below, costa frequently of lighter color, (1.5–)2–6.3 cm. long × 1.5–4.5 mm. broad, 5 to 15 times as long as broad. Racemes spiciform as usual, ca. 5–14 cm. long, multiflorous; petals 2.5–3.5 mm. long; ovary stipitate, villous. Legume straight, 8–20 cm. long × 0.7–1.3 cm. broad, rarely subfalcate, compressed to subterete, submoniliform, glabrous, straw-yellow or tinged with violet, short-stiped, with strong, short, or elongate acumen, ca. 5–18-seeded; joints subquadrate to oval; seeds oblique to longitudinal.

DISTRIBUTION. Southwestern United States and Mexico.

COMMON NAMES. Honey mesquite; mesquite. In India: bilayati kikar (Punjab).

SELECTED MATERIAL EXAMINED. **U.S.A.** CALIFORNIA: Inyo Co., Furnace Range, *Train 653* (SI). OKLAHOMA: Major Co., *Goodman & Waterfall 4212* (NY); Woods Co., *S. Stephens 21639* (NY), *G. W. Stevens 580* (MO); Wichita Mountain, *Robbins 2854* (NY); Cimarron Co., Kenton, *Rogers 5936* (US). KANSAS: Stokes Hill, *L. F. W.*, 15 IX 1897 (US); Comanche Co., *R. S. Kellogg*, 27 VII 1903 (US). NEVADA: Las Vegas, *Arsène 18892* (R). NEW MEXICO: Dog Springs, *Mearns 2325* (NY, type of *Neltuma neomexicana*); Logan, *Bailey 498, 499* (US); Western Plains to El Paso, *Wright 155* (US); Socorro Co., Truth, *B. Vogel*, 8 VI 1962 (COLO). TEXAS: *Lindheimer II-233, III-382* (MO, US); *M. A. Carleton*, 1891 (SI 5472, US); Laredo, *Heddle 2794* (SI), *Lundell 13801* (US), *Guerra et al. 613*, *Botello & Ayala 32*, *Ramos & Murillo 96* (COLO); Reeves Co., Pecos City, *H. Eggert*, 5 VII 1900 (MO); Hood Co., Granbury, *E. J. Palmer 6514* (MO); Taylor Co., NW of Abilene, *Mahler 3619* (MO); Grayson Co., Denison, *E. J. Palmer 14274* (MO); Dallas, *Stephenson 240*, *Reverchon 4331* (US), *Lundell & Lundell 85* (US), *8571* (TEX); Presidio Co., *Hinckley 1509* (NY); Pecos Co., *Cory 51939* (US), *Tharp 43610* (SI, US), *43660* (SI); Childvess, *Coville 1851* (US); Brownsville, *H. S. Barber* (US); *H. S. Gentry 6683* (US); Tom Green Co., *Tweedy 87* (US); Austin, *Tharp 8520* (US), Standley, *A. Ruth 16* (SI); Calhoun Co., Port Lavaca, *Cory 51122* (US), *Fisher 41081* (LIL, SI); Willacy Co., *M. C. Johnston 54542*, Winckler Co., *Stuessy 150* (TEX); Kleberg Co., *M. C. Johnston 54360* (COLO); Laredo, *C. J. Lundell 13801* (TEX); Uvalde Co., *C. W. Johnson 50–126* (LIL); San Antonio, *Burr 318* (LIL); Laredo, *Chute M-3* (MEXU); Dallas Co., *Wagner 77* (TEX); Uvalde Co., *Johnston & Muller 2* (TEX); Texas, without further locality, *Ledingham 466* (NY). **Mexico:** Coahuila, Saltillo, *E. Palmer 26* (UC); Saltillo, road to Torreón, *S. S. White 1668* (SI); Coahuila, *Gentry et al. 20041*, *Rose & Hay 5250* (US), *Wynd 741* (US); Coahuila, Sabinas, *M. C. Johnston 5886* (MEXU); Tamaulipas, *Goldman 729* (US); Chihuahua, Santa Eulalia, *Wilkinson*, 11 VII 1885 (US); Vera Cruz, Pueblo Viejo, *E. Palmer 550, pro parte* (US); Yucatán, Progreso, *Goldman 605* (US); Nuevo León, S of Monterrey, *M. C. Johnston 5301* (MEXU). **Puerto Rico:** planted, *Britton & Britton 9056*

(NY). **South Arabia:** Aden, *Mearns 9* (US). **Burma:** Mandalay, cultivated. *O. E. White 388* (UC, US). **India:** Punjab, salt range, Camp Kusah, *Bis Ram 838* (GH). **Pakistan:** Karachi University, cultivated, *S. M. Ashra Fridi 80* (MO). **Australia:** Queensland, Darling Downs District, Yandilla, *S. L. Everist*, 28 V 1953 (GH, US).

USES. Similar to those of related species; according to Howes (Vegetable Gums and Resins 65. *fig. 11.* 1949 (sub *P. juliflora*)), the most important gum-producing plant in North America.

Prosopis glandulosa var. **torreyana** (Benson) Johnston, Brittonia 14: 82. 1962; Isely, Madroño 21: 293. 1972.

Prosopis juliflora (Sw.) DC. var. *torreyana* Benson, Am. Jour. Bot. 28: 751. *fig. 4.* 1941.

General habit like that of var. *glandulosa*; spines equal, solitary or paired on the same branchlet; flowering twigs often without spines. Leaves glabrous, unijugate, rarely bijugate; petiole (including rachis when extant) 1–8 cm. long; pinnae elongate, 8 to 24 pairs, 5–8 mm. distant on the rachis, but often less than in the type variety; leaflets linear, mucronulate, glabrous, 0.7–2.5 cm. long (mostly 1.5–2.5 cm.) × 1.5–6 mm. broad, 5 to 9 times as long as broad, prominently veined below. Racemes and flowers as usual; rachis to 12 cm. long. Legume straight, compressed, thickly submoniliform or subtorulose, 7–18 cm. long × 0.7–1.1 cm. broad, glabrous, yellow, often violet-tinged; seeds oval, 6–7 mm. long.

DISTRIBUTION. Southwestern United States, Mexico. See discussions by Johnston (1962) and Isely (1972), cited above.

COMMON NAMES. Western honey mesquite; mesquite.

MATERIAL EXAMINED. **United States.** NEVADA: Clark Co., Lees Canyon, *Balls & Straw 19298* (LIL); Nevada, without further locality, *Clokey 8396* (LIL, MO). CALIFORNIA: S. Bernardino Co., *Munz 15552*; Imperial Co., Colorado Desert, *Johansen & Ewan 7135* (SI); Death Valley, *Solbrig 2304* (SI). ARIZONA: Apache Junction, *Gillespie 8441*, Mohave Co., Vulcans Throne, *Cottam 13017*, Yuma, *E. O. Wooton*, fl., 21 IV 1913, Chiricahua Mts., *Blumer 1255*, Cochise Co., Portal, *Eggleston 10958* (COLO). ARIZONA: Coconino Co., *Clover 5085* (SI). NEW MEXICO: 34 miles E of Engle, *Cutler 2018* (MO, SI). TEXAS: Presidio Co., *Hinckley 1476*, *Cory 53581* (SI); Rio Grande, 6 miles E of Castolon, Brewster Co., *Cutler 1874* (SI), *Thompson 52-225* (LIL); Pecos Co., Fort Stockton, *Cory 51939* (SI). **Mexico:** Baja California, *Wiggins & Gillespie 4051*, Cabo S. Lucas, *Shreve 7259*, La Ventana a S. Antonio, *Carter 2642* (US); Vera Cruz, Pueblo Viejo, *E. Palmer 550, pro parte* (US); Coahuila, La Ventana, *Nelson 3931* (US); Sonora, Las Bocas, coastal, sandy flat xerophytic tree-cactus forest, *Solbrig 4402 & Ornduff* (SI).

Prosopis glandulosa var. **prostrata** Burkart, var. nov.

A var. *glandulosa* differt solummodo habitu prostrato, caulibus subterraneis horizontalibus validis longaevis, ramis aereis prostratis, haud vel rarius tarde arboreis.

TYPUS VARIETATIS: Texas, Kleberg County, western part of Laureles Division of King Ranch, black clay, prairie with much "running mesquite," *M. C. Johnston 54359*, fl., 15 IV 1954 (COLO).

Similar to var. *glandulosa*, but prostrate with strong underground, horizontal branches; aerial branching prostrate, never or only seldom and slowly becoming arborescent; spines seen 0.7–2 cm. long; solitary twigs reddish. Leaves unijugate, as in var. *glandulosa*.

COMMON NAMES. Running mesquite; in Spanish (Mexico), mesquite rastrero.

DISTRIBUTION. U.S.A. (Texas); Mexico (Tamaulipas).

OBSERVATIONS. Already well characterized, but not described, by M. C. Johnston in his important paper on North American Algarobiae (Brittonia 14: 76, 77. 1962). A parallel variation exists in *Prosopis laevigata*, according to Johnston, but I have not seen such material.

This is an impressive case of an arborescent *versus* shrubby habit in very closely related species, exemplified in South America by the similar, vicarious species-pair *Prosopis flexuosa* (arboreous) and *P. alpataco* (shrubby).

In the specimen *H. von Schrenk 45* (MO), from Marathon, Brewster Co., Texas, of var. *glandulosa*, there are visible transitions between the normal axillary spines and lateral shoots, as I found earlier in Argentine species of sect. ALGAROBIA, ser. Chilenses (Burkart, Darwiniana, 1937).

41. **Prosopis alpataco** R. A. Philippi, Sertum Mendocinum, Anal. Univ. Chile 21: 394. 1862; Philippi, Linnaea 33: 62. 1864; Burkart, Darwiniana 4: 108. *pl. 23*. 1940; Burkart, in Cabrera, Fl. Prov. Buenos Aires 3: 430. *fig. 134, A–B*. 1967.

Prosopis stenoloba Philippi, Catal, praev. plant. Tarapacá, Anal. Mus. Nac. Chile, 2nd. sect. Bot. 20. 1891.

Prosopis juliflora (Swartz) DC. forma *fruticosa* Hauman, Anal. Mus. Nac. Buenos Aires **24:** 391. 1913.

Prosopis alba Grisebach forma *fruticosa* (Hauman) Monticelli, Lilloa 3: 347. 1938.

Shrub, spiny, glabrous, 20 cm.–3 m. tall; aerial shoots commonly thin, erect, flexuous, dispersed over a round surface up to 10 m. in diameter, starting from thick, horizontal, subterranean branches which do not develop adventitious roots but spread from a central, primary, axonomorphic, vertical tap root; spines axillary, geminate, uninodal, 0.3–6 cm. long, sometimes solitary or members of an unlike pair (one spine smaller). Leaves uni- to rarely bijugate, lax, deciduous; petiole (including rachis when extant) 0.7–9.5 cm. long; pinnae 3–14 cm. long, often arched when dry; leaflets linear, distant, 9–17(–25) pairs per pinna, opposite, mostly glabrous, obtuse or subacute, 0.5–1.7(–3) cm. long (1–1.1 cm. in the type specimen) × 0.9–1.5(–3.5) mm. broad, subcoriaceous; veins little de-

veloped below. Racemes dense, ca. 6–14 cm. long; peduncle short. Legume linear, compressed, straight, subfalcate or rarely subannular or S-shaped, with parallel sutures, or undulate and submoniliform; stipe and acumen very short, straw-yellow in the typical form but frequently violet-tinged, 7–17 cm. long × 0.6–1.2 cm. broad × ca. 0.5 cm. thick; pulp scarce, bitter or sometimes sweet; endocarp articles 8 to 18, indehiscent, hard, subquadrate to ovoid, ca. 8.5–11 mm. long × 9–10 mm. broad.

DISTRIBUTION. West-central Argentina, especially in the arid so-called "Monte" Province, characterized by *Larrea* species.

COMMON NAME. Alpataco, from the Indian alpa (earth) and taku (carob tree), indicating the subterranean growth of the main branches; sometimes lámaro (San Juan, Mendoza), used more often for *P. flexuosa*.

NEW MATERIAL EXAMINED. **Argentina.** LA RIOJA: Rosario vera Peñaloza, *Piccinini & Leguizamón 1710* (BAB, SI), Salinas de Macasín, *Sayago 2428* (SI). SAN JUAN: Calingasta, La Isla, *Mireya Vila 6*, Angaco Sud, *J. C. Tinto*, Herb. Forestal *2011* (SI); S. Juan a Calingasta, *Sayago 2440* (SI); Dept. Iglesia, *J. H. Hunziker & O. Caso 4675, 4682, 4683, 4692* (SI); Camino S. Juan a Mendoza, Media Agua, *Nicora 4297* (SI). MENDOZA: Cerro de la Gloria, *Mexía 4374* (GH, MO); Luján de Cuyo, *Semper 133* (NY), *Biloni M-105* (SI); Maipú, médanos, *Ruiz Leal 9930* (SI), *Bartlett 19360* (GH); Las Heras, *Semper 214* (NY); Uspallata, *Covas 15060, 15108* (SI); Borbollón, *J. H. Hunziker 3159* (BAB, SI), *Krapovickas & Cristóbal 14606* (CTES, SI); Río Atuel, *Kurtz 7448* (CORD, R); Rivadavia, *Ruiz Leal 10592* (SI); San Rafael, El Cerrito, *Bartlett 19445* (GH); Volcán Diamante, *Ruiz Leal 17006* (SI), *Martínez Crovetto & Piccinini 6269* (BAB, SI), *Boelcke et al. 15524* (BAB, SI); La Paz, *Ruiz Leal 9451, 11825* (SI); Dept. Lavalle, *Ruiz Leal 13840, 14523* (SI); Malargüe, *Ancibor, Cano, & Crespo* (BAB 90122, SI), *Burkart, Troncoso, & Nicora 14144–14146* (LIL, SI); Las Heras a Lavalle, *Ruiz Leal 9796* (LIL); Mendoza, without further locality, *Semper 239* (NY). NEUQUÉN: Plaza Huincul, *Cabrera 11006, 11059* (LP, SI); Añelo, *Morello 10, 12* (SI); Buta Ranquil, 1100 m. elev., *Ruiz Leal 22391* (SI); Confluencia, *O'Donell 1874* (GH). CÓRDOBA: General Roca, Huinca Renancó, *A. T. Hunziker 9383* (SI); General Roca, Villa Huidobro, Cañada Verde, *Schulz 6005* (LIL). SAN LUIS: sierra, *A. T. Hunziker 9304* (SI); Nueva Escocia, médanos, *Burkart 10850* (SI); San Luis, without further locality, *Covas 1087* (NY). LA PAMPA: Limay Mahuida La Reforma sobre el Río Salado, *Solbrig 189*, General Acha, *Solbrig 180* (SI); Realicó, *Schulz 5860* (LIL, NY, SI); Laguna La Amarga, *Burkart 15952* (SI); Río Colorado frente a J. de Garay, *Burkart 15860* (SI). RÍO NEGRO: Valcheta, *T. Meyer 7194* (LIL), *7220*, Nihuel Niyén, *T. Meyer 7258* (SI); Chelforó, orillas Río Negro, *Mroginski & Fernández 22575* (SI); San Antonio Oeste, Correo, *Movia & Mendonza 2565* (SI); Choele-Choel, *Cabrera 18619* (SI); General Roca, *Soriano 1240* (SI); Oeste de Río Colorado, *Burkart 15845* (SI); Pichi Mahuida Río Colorado, *O'Donell 1535* (NY). CHUBUT: Puerto Madryn, *Crespo & Troncoso 1588, 1593* (SI); Travesía de Rawson a la Cordillera, *Illín 188* (UC). BUENOS AIRES: Bahía Blanca, *Grünbein, Fabris, & Schwabe 4835* (SI); L. Rosales, Pehuen-Co., dunas, *Burkart 25629, Cabrera & Fabris 14915, Boelcke et al. 11939* (SI); Villarino, Médanos, *Boelcke et al. 11774, 11794, Burkart 25650* (SI); Pedro Luro, *Bartlett 19925, 19926* (SI); Patagones, La Pantanosa, *Krapovickas 1979* (LIL, SI); Carmen de Patagones, *T. Meyer 6989* (GH, LIL, SI), *Boelcke 1673, Soriano 1568* (SI).

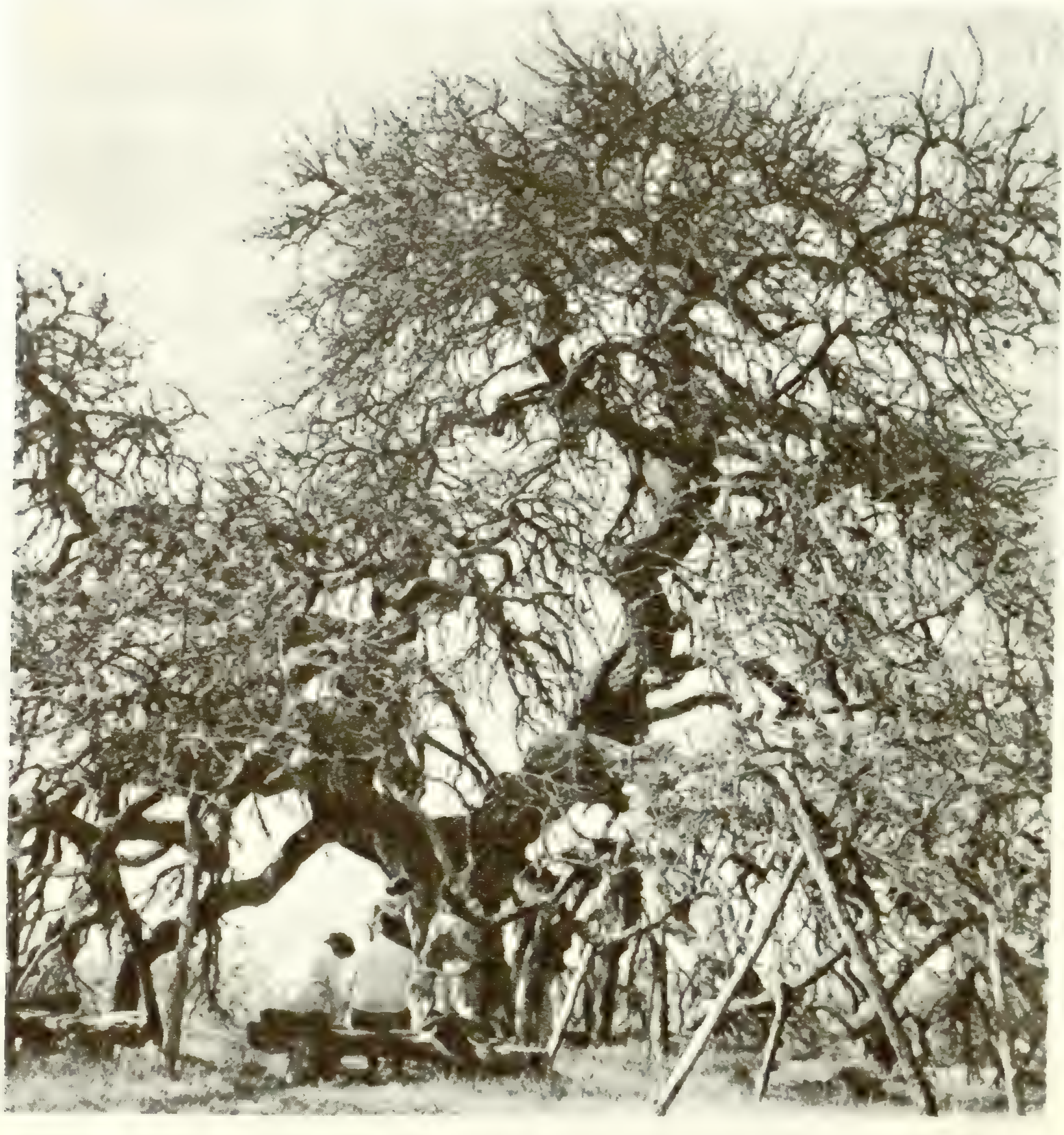

FIGURE 12. **Prosopis.** A specimen tree of *P. alba*, approximately 200 years old and probably a relic of the primitive forest. This tree, growing in the Quinta Pueyrredón, barranca of San Isidro, Prov. Buenos Aires, Argentina, has been named a national monument. It was under this tree that the generals San Martín and Pueyrredón conferred in 1816 to formulate a plan for liberating the country. *Photo.* from the newspaper *La Prensa* of Buenos Aires, March 26, 1961.

OBSERVATIONS. *Prosopis alpataco* is a widespread and characteristic endemic in western Argentina, mainly recognizable by its shrubby habit with underground branches, otherwise very close to *P. flexuosa* DC., which grows in the same Monte region, but is arboreal. *Prosopis alpataco* is somewhat variable in its fruit and foliage, but it does not seem rewarding to distinguish varieties.

C. Muñoz Pizarro, Syn. Fl. Chile 153. *pl. 133.* 1959, mentions *Prosopis alpataco* from northern Chile, giving a good illustration. I venture to think

that this material is *P. flexuosa* DC. (formerly described from that region as *P. fruticosa* Meyen).

Some large-leaved forms of *Prosopis alpataco* show great similarity with *P. glandulosa* from western North America, but with herbarium material it is difficult to ascertain identity in habit and fruit characters, which seem to mark the differences. This similarity is the reason why authors repeatedly cited *P. juliflora* for both regions; see P. C. Standley, Jour. Washington Acad. Sci. 6: 239. 1916, where *P. juliflora* is mentioned doubtfully for Río Negro, Argentina, and is compared with *P. glandulosa* Torrey from New Mexico.

42. **Prosopis alba** Grisebach, Plantae Lorentzianae in Abh. Kön. Ges. Wiss. Göttingen 19: 83. 1874; Grisebach, Symb. Fl. Arg. *Ibid.* 24: 118. 1879; Hieronymus, Icones et Descript. Plant. R. Argent., Actas Acad. Ci. Córdoba 2(1): 5. *pl. 1.* 1886; Burkart, Darwiniana 4: 119. *fig. 14, pl. 19.* 1940; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. *2.* 132 *et passim.* 1952; Tortorelli, Maderas y Bosques Argentinos 392. Buenos Aires. 1956; Burkart in Cabrera, Fl. Prov. Buenos Aires 3: 429. 1967.

Prosopis siliquastrum (Cav.) DC. var. *longisiliqua* Philippi, Catalog. praev. plant. Tarapacá, Anal. Mus. Nac. Chile, 2nd sect. Bot. 20. 1891.
Prosopis atacamensis Philippi, Anal. Univ. Santiago (Chile) 84: 444. 1894; Burkart, Darwiniana 4: 119. 1940.

Tree 5–15 m. tall, in age the short trunk possibly reaching 1 m. in diameter; treetop rounded; branchlets drooping; spines scarce and small, only on strong shoots, 2–4 cm. long, geminate. Leaves rather large, uni- to trijugate, glabrous; petiole (including the rachis) 0.5–8 cm. long; pinnae 6–14 cm. long, with 25 to 50 pairs of leaflets, these linear, acute or subacute, in some forms nearly obtuse, 0.5–1.7 cm. long × 1–2 mm. broad, scarcely nerved below, approximate, 1.5–6 mm. between pairs. Racemes spikelike as in similar species, 7–11 cm. long; florets greenish-white to yellowish, small; calyx 1 mm. long, puberulous; corolla 3–3.2 mm.; stamens 4.5 mm.; pistil 5 mm. long. Legume falcate to ring-shaped (ring ca. 7 cm. in diameter), linear, compressed with parallel margins, straw-yellow, stipitate and acuminate, 12–25 cm. long × 11–20 mm. broad × 4–5 mm. thick, with 12 to 30 subquadrate endocarp segments broader than long, ca. 0.6 × 1 cm.

DISTRIBUTION. Plains of subtropical Argentina to Uruguay, Paraguay, southern Bolivia, to Peru.

COMMON NAMES. Algarrobo blanco; igopé or ibopé-pará (Guaraní).

NEW MATERIAL EXAMINED. **Bolivia:** La Paz, Río Abajo, *Buchtien 3187*, 2700 m. elev. (NY). **Argentina.** JUJUY: Yuto, *Carmelich, Devoto, & Rial Alberti*, Herb. Forestal *584* (SI); San Pedro, *Devoto & Rial Alberti*, Herb. Forestal *565* (SI). SALTA: Saucelito, *Ragonese & Cozzo*, Herb. Forestal *2630*; Jaquiasmé, *Devoto & Rial Alberti*, Herb. Forestal *1137*, *1143* (SI); El Fraile a Alemanía,

Schulz 11480, Hickmann, Pozo El Milagro, *Maruñak et al. 544* (SI); Rosario de la Frontera, *Burkart 20371* (SI); Dept. S. Carlos, Angastaco, *Krapovickas & Cristóbal 20640* (SI); Ruta 9, Río Juramento, *T. Meyer 22644* (SI); Curtiembre a Peña de Testa, 1300 m. elev., *Meyer & Legname 23137* (LIL, NY). SANTIAGO DEL ESTERO: Dept. Robles, Beltrán, *Maldonado 476*, *B. Vuilleumier 1031–1*, Beltrán, *B. Vuilleumier 1031–5* (SI); Colonia Giménez, *Lima 1387* (LIL); Capital, *T. Meyer 6883* (GH); La Banda, *García 815* (UC); Parque Aguirre, *López 1* (SI). CÓRDOBA: Dept. Río Seco, Villa Candelaria, *Sayago 54*; Calamuchita, *Sayago 3674, 3675* (SI); Capital, *Báez 29*, Observatorio, *J. H. Hunziker 2648* (SI); Dept. Río I., La Posta, *Sayago 1706* (SI); San Justo, Vacas Blancas, *Sayago 3635–37* (SI); S. Francisco del Chañar, *Balegno 333* (NY); Villa María, *B. S. Simpson 1039* (GH, SI, TEX). SAN LUIS: Quines, *J. R. Báez*, I 1941, Aguada de Pueyrredón, *Báez 17* (SI); Bajo de Velis, *Kurtz 8450* (R). FORMOSA: E. del Campo, *Maradona 2, 51* (SI); Dept. Patiño, *Palacios 314, 315, 317, 323, 329, 330, 464, 488* (SI); Pirané, *Morel 327* (SI); Mojón de Fierro, *Krapovickas 1088* (SI); Formosa, without further locality, *Rojas 12258* (NY). CHACO: Resistencia y Colonia Benítez, *Schulz 1339, 1346, 11320* (SI), *Martínez et al.* (BAA 9418, 9596). SANTA FE: Vera, *Burkart 5929*; Videla, *Courault & Ragonese 2074*, Malabrigo, *Burkart 5928, 5936*, Reconquista, *Burkart 5932* (SI). CORRIENTES: Dept. Saladas, Río S. Lorenzo, *Schwarz 9095* (SI); Empedrado, *Pedersen 3051* (NY). ENTRE RÍOS: Paraná, *T. Meyer 10028* (LIL); La Paz, *Burkart et al. 23355* (SI); Victoria, barrancas, *Burkart 8603, 8672, 17719, 17673, 17686* (SI). BUENOS AIRES: Partido Baradero, Alsina, *Krapovickas 3311* (LIL, SI, SP). **Uruguay:** Montevideo, cultivated(?), *Fruchard*, X 1876 (NY).

Prosopis alba var. **panta** Grisebach, Symb. Fl. Arg. in Abh. Kön. Ges. Wiss. Göttingen **24**: 118. 1879; Burkart, Darwiniana **4**: 121. *lám. 20*. 1940.

Prosopis panta (Grisebach) Hieronymus, Bol. Acad. Nac. Ci. Córdoba **4**: 284. 1882.

Prosopis alba var. *panta* is distinguished from var. *alba* mainly by the nearly straight legumes, but there is a marked variation in foliage, so that with better studies another variety may be established, characterized by larger and more obtuse leaflets, reddish branchlets and sometimes very large legumes. This form predominates in northwestern Argentina and enters southern Bolivia; in the eastern Gran Chaco and Paraguay a form with smaller leaflets is common.

Legumes up to 30 cm. long × 1.8 cm. broad, fleshy, sweet, of the best kind for food or forage.

COMMON NAMES. Algarrobo panta; algarrobo impanta.

MATERIAL EXAMINED. **Peru:** Dept. Huancavelica, Prov. Tayacaja, Mayocc, *Tovar 4835* (SI). **Bolivia:** Tarija, Cercado, 1900 m. elev., *T. Meyer 17964* (LIL, SI). Tarija a Padcaya, 2000 m. elev., *Meyer, Legname & Cuezzo 22960, 22962* (LIL); Songo, *Bang 823* (NY, MO); Bolivia, loc(?), *Weddell 1848*, *Bois* no. *VIII*, *Catal. 4814* (P, SI). **Argentina:** JUJUY: Yuto, *Carmelich & Rial Alberti*, Herb. Forestal *580* (SI). SALTA: Lomas de Olmedo, *Devoto & Rial Alberti 2367* (SI); La Zorra, *Carmelich et al. 1012*; Montealto, Orán, *Rodríguez 1152* (SI); Coronel Moldes, *T. Meyer 3548* (GH, UC); Hickmann, Pozo El Milagro, *Maru-*

ñak et al. 547, Coronel Cornejo, *Maruñak et al. 581* (SI); Valle de Lerma, Cerrillos, *Parodi 13521* (SI). TUCUMÁN: Tiopunco, 2000 m. elev., *R. Schreiter* (LIL 54713/14 in SI, form with blackish pods called "panta negra"). CÓRDOBA: Dept. San Justo, Marull, *Sayago 1691* (SI); San Luis, Quines, *J. R. Báez*, I 1941 (SI 26984). CHACO: Colonia Benítez near Resistencia, *A. G. Schulz 1340–1344, 1347* (SI). CORRIENTES: Dept. Concepción, *Cano & Cámara 751* (BAA), *Cano 2131* (BAB); San Luis del Palmar, *Quarin et al. 537* (ENCB, SI); Mburucuyá, *Pedersen 1412* (MO). SANTE FE: northern part, Vera and Malabrigo, *Burkart 5904, 5930, 5937* (SI). ENTRE RÍOS: Paraná, Parque San Martín, *Báez 7, 8, Doello Jurado*, IV 1939 (BA 32039, SI). **Paraguay:** Sector Puerto Casado, Km. 160, *Rojas 8452* (SI); Sector Lopez de Filippis, Chaco paraguayo, *Rojas 8407, 8314a, 8418, 8437* (SI).

USES. A very important tree in arid lands, similar in value to *Prosopis chilensis*, *P. nigra*, or *P. pallida*. In northeastern Argentina native people frequently call it "el árbol," the tree, because of its usefulness and abundance. It is cultivated to a limited extent. (For Argentina, see Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. 135. 1952 (Ing. Castañeda Vega in the plains of Prov. Córdoba); for northern Chile, see H. Medina, Rev. Arg. Agron. **8**: 25–48. 1941.) In the Chaco it furnishes timber of high value for construction, doors, premanufactured houses, etc. Trees with straight trunks 8 to 10 m. tall occur, but these are becoming extremely rare, from being cut in preference to the other shorter ones. Thus a negative, artificial selection is taking place, which shoud be counteracted by genetic up-building of the best lines in experimental plots. (Information on uses in the Chaco was furnished by Dr. Augusto C. Schulz, Colonia Benítez, Chaco).

43. **Prosopis velutina** Wooton, Bull. Torrey Bot. Club **25**: 456. 1898; Johnston, Brittonia **14**: 86. 1962; Isely, Madroño **21**: 295. 1972.

Prosopis juliflora (Sw.) DC. var. *velutina* (Wooton) Sargent, Silva N. Am. **13**: 15. 1902; Standley, Trees and Shrubs of Mexico, Contr. U. S. Natl. Herb. **23**(2): 353. 1922; Benson, Am. Jour. Bot. **28**: 750. 1941.

Prosopis chilensis (Mol.) Stuntz var. *velutina* (Wooton) Standley, Additions and Corrections, Trees and Shrubs of Mexico, Contr. U. S. Natl. Herb. **23**(5): 1658. 1926.

Neltuma velutina (Wooton) Britton & Rose, N. Am. Fl. **23**(3): 186. 1928.

Tree up to 15 m. high; trunk short; spines axillary, geminate, 1–2 cm. long, all vegetative parts more or less pubescent. Leaves uni- to bi- (or tri-)jugate, puberulous; petiole plus rachis, when extant, 0.6–6 cm. long × 0.8–1.2 mm. in diameter; pinnae 2–9 cm. long; leaflets oblong, pubescent, ciliolate, 12 to 30 pairs per pinna, approximate, obtuse, nervate below, coriaceous, 4–13 mm. long × 2–4 mm. broad (3.5 to 4 times as long as broad). Racemes spikelike, 5–15 cm. long; florets short-pedicelled, somewhat pubescent outside, especially on the calyx; petals 2.5 mm. long, the tip villous within. Legume linear, 8–16 cm. long × 6–10 mm. broad, flattened, straight or falcate; margins shallowly undulate, the stipe 2–10 mm., the beak 2–11 mm. long, legume "very velutinous when young and

pubescent even in age"; endocarp segments ca. 10 to 17, ovoid-subquadrate, about as long as broad; seeds ovate, 5–7 mm. long; sometimes the legume smaller, compressed-moniliform, and reddish, in what may be a variety or a *P. articulata* introgression (*White 402*, GH).

DISTRIBUTION. Mexico, NW states (Sonora); rare in neighboring United States (Arizona).

COMMON NAMES. Velvet mesquite; mesquite.

MATERIAL EXAMINED. **Mexico:** Sonora, Mexican Boundary Survey 300*a*, between Colorado and Santa Cruz rivers, *Schott* (NY); Hermosillo a Tastiota, El Zapo, *Wiggins & Rollins 277* (LIL, NY); NE Sonora, Monctezuma, *S. S. White 402* (GH); Sonora, Pesqueira, *Maltby 247* (TEX). **United States.** ARIZONA: Cochise Co., *B. Vuilleumier 2228–1* (TEX); Fort Huachuca, *Wilcox*, V 1892, Hallup, *Pringle*, 3 VIII 1894 (NY); Pima Co., Pantano Wash, N of Vail, *Venrick 549* (MO); Tucson, Pima Co., *Warren & Turner 68–157* (ENCB); Tucson, *Ehlers & Ehlers 6396* (MEXU); Coconino Co., *Demaree 44311* (NY); Ajo, S. Maricopa Co., *Rossbach 5046* (R); valley near Camp Lowell, *Pringle*, May 13, 1883, sub *P. juliflora* (SGO); Arizona, without further locality, *Pringle 13665*, 23 IV 1881, lectotype selected by Britton and Rose (Mimosaceae in N. Am. Fl. **23**(3): 186. 1928) (MO, NY). **Australia** (cultivated plants): N. S. Wales, Broken Hill S., *Garvick 4* (US); Queensland, Warrego District, Comougin, *Everist 5902* (US); N. S. Wales, Trangie Exp. Farm, *Whittet 10581* (US).

44. Prosopis pugionata Burkart, Darwiniana 9: 70. *figs. 1–3.* 1949; Burkart, Las Leguminosas Argentinas, silvestres y cultivadas. ed. 2. 131. 1952.

Tree 2–8 m. high, glabrous, very spiny; trunk 1.5–2 m. long, ca. 20–30 cm. in diameter; bark dark, rugose; top rounded; branchlets flexuous; spines axillary, uninodal, geminate, conic-subulate, strong, smooth, on vigorous shoots 2–9.5 cm. long × 7 mm. in basal diameter without strangulation at base, on weak shoots much smaller or absent; foliage light, deciduous. Leaves uni- or bijugate, ample, mostly fascicled; petiole 0.5–2 cm.; pinnae 1.5–6.5 cm. long; leaflets linear, glabrous, opposite, 11 to 25 pairs per pinna, distant on the rachis (1–6 mm.), 3.5–8(–10) mm. long × 0.6–1 mm. broad, obtuse or subacute, unicostate; lateral nerves not visible. Racemes as in similar species of sect. ALGAROBIA, 8–9 cm. long; florets nearly glabrous outside; petals 3 mm. long, their tips villous within; ovary villous. Legume linear, compressed, submoniliform, tinged with violet, straight, 9–11.5 cm. long × 8–10 mm. broad, edible, with 12 to 16 subquadrate to ovate endocarp segments.

DISTRIBUTION. West-central Argentina, especially in the region around the Salinas Grandes.

COMMON NAMES. Algarrobo de las Salinas; alpataco; algarrobo.

MATERIAL EXAMINED. **Argentina.** CÓRDOBA: Dept. Tulumba, La Majadilla a La Esperanza, *Sayago 1685* (CORD, SI); San José, *Sayago 2626, 2627* (SI); Dept. Pocho, Sierra de Pocho frente a Chancaní, *Sayago 1442, 1443* (SI); Chan-

caní, *Ragonese 9331* (BAA, SI); Dept. Pocho o San Alberto, camino de Villa Dolores a Chancaní, *A. T. Hunziker 12930, 11510* (CORD, SI); Dept. Tulumba, N of Quilino, Ruta 60, Km. 880, *B. Timmermann*, 30 IX 1972 (TEX). LA RIOJA: Dept. Rivadavia, estancia La Esperanza, *C. D. Ocampo*, VIII 1955 (CORD); Dept. R. Vera Peñaloza, de Chepes hacia San Juan, *A. T. Hunziker 12255* (SI). CATAMARCA: Dept. Capital, *E. A. Ulibarri 493* (SI). SAN JUAN: Dept. Iglesia, SW of Rodeo, *Bartlett 20541* (SI). SAN LUIS: Dept. Belgrano, Hualtarán, *Anderson 1399* (SI).

OBSERVATIONS. This species is closely related to *Prosopis flexuosa* DC., which has short spines and broader leaflets; *P. alpataco* Philippi, with shrubby habit and underground branching; and *P. horrida* Kunth, with bi- or trijugate leaves and broad leaflets, characters which separate *P. pugionata* also from *P. nigra* (Grisebach) Hieronymus.

NAMES OF SPECIES EXCLUDED FROM PROSOPIS

Prosopis adstringens Steudel = **Acacia atramentaria** Bentham
P. benthami Chodat & Wilczek = **Prosopidastrum globosum** (Hooker & Arnott) Burkart
P. bonplandiana (Kunth) Sprengel = **Entada polystachya** DC.
P. dubia Guillemin & Perrottet = **Acacia sieberiana** DC.
P. dubia H.B.K. = **Enterolobium cyclocarpum** Grisebach
P. elegans Sprengel = **Piptadenia** spp., **P. rigida** Bentham vel **P. trisperma** Bentham
P. elephantorrhiza Sprengel = **Elephantorrhiza burchelli** Bentham
P. ephedroides Gillies ex Hooker & Arnott = **Mimosa ephedroides** Bentham
P. esquirolii H. Léveillé = **Pterolobium punctatum** Hemsley
P. faeculifera Desvaux = **Parkia africana** R. Brown
P. gilliesii Mackloskie = **Caesalpinia gilliesii** Wallich ex Hooker
P. globosa Gillies ex Hooker & Arnott = **Prosopidastrum globosum** (Hooker & Arnott) Burkart
P. globosa var. *mexicana* Dressler = **Prosopidastrum mexicanum** (Dressler) Burkart
P. herzogii Harms = **Parapiptadenia** cf. **excelsa** (Grisebach) Burkart
P. heterophylla Bentham = **Acacia willardiana** Rose
P. insularum (Guillemin) Breteler, Acta Bot. Neerl. **9:** 397–403. 1960 = **Schleinitzia insularum** (Guillemin) Burkart, comb. nov., based on *Acacia insularum* Guillemin, Ann. Sci. Nat. Paris II. **7:** 360. 1837.
P. fischeri Taubert = **Pseudoprosopis fischeri** (Taubert) Harms
P. kirkii Oliver = **Acacia albida** Delile
P. microphylla H.B.K. = **Acacia tortuosa** Willdenow
P. odorata Torrey & Fremont, 1845. The type material was a mixture of flowering twigs of *P. glandulosa* (so *P. odorata* becomes its synonym) with added legumes of *P. pubescens* Bentham. See Benson, Madroño **15:** 53. 1959.[4]

[4] Professor Burkart seems to have accepted the statement of Torrey concerning the composition of Fremont's collection and its identification. Benson's 1959 conclusions and Isley's statement of 1972 (**Madroño 21:** 295) seem, however, to be more appropriate. *Prosopis odorata* becomes a synonym of *P. glandulosa* var. *torreyana*. *Prosopis odorata* was lectotypified by Isely. *Prosopis pubescens* was published a year after *P. odorata* and may be identified easily from its description. BGS.

P. scandens Stokes = **Entada scandens** Bentham
P. striata Bentham = **Prosopidastrum globosum** (Hooker & Arnott) Burkart
P. tamariscina Sprengel = **Gagnebina tamariscina** DC.

RESUMEN

Monografía del género *Prosopis* Linn., emend. Bentham y emend. Burkart (Leguminosas–Mimosóideas). Basándose en sus estudios anteriores (véase Darwiniana 4. 1940) y contribuciones varias, el autor presenta una revisión completa de las especies de *Prosopis* (algarrobos americanos, mesquites y afines) en su distribución mundial. Se lo considera un grupo filogenéticamente antiguo dentro de la subfamilia, con distribución vasta a través de tres continentes: desde Asia sudoccidental y Africa a América occidental cálida, desde Estados Unidos sudoeste hasta Patagonia. Se distinguen 44 especies, de las cuales sólo 4 pertenecen al viejo mundo, siendo las demás americanas, con dos centros principales en las regiones áridas y semiáridas de México y de la Argentina, siendo éste último el país con mayor número de especies (28 en total, de ellas 13 endémicas).

Se traza la historia taxonómica del género, se discute su morfología y filogenia, su subdivisión en secciones y series, su distribución por países y centros de polimorfismo a escala universal, su importancia ecológica y económica, mencionando las múltiples utilidades que presta en regiones de clima cálido-seco y se propicia su mayor estudio desde el punto de vista biológico y ecológico, tal como el que se lleva a cabo en colaboración, entre botánicos de Harvard University, la Smithsonian Institution y la Universidad de Buenos Aires. Como meta final se aconseja la inclusión de las mejores especies y razas seleccionadas de estos valiosos árboles en programas de reforestación en zonas áridas.

La parte principal del trabajo está destinada a aclarar la taxonomía del género, a distinguir sus 44 especies mediante una clave dicotómica y descripciones complementarias, algunas ilustraciones, y a dilucidar su nomenclatura correcta y sinonimia. Aparte de una sección nueva, se crean nuevas series, una nueva especie de Irán, un nuevo nombre para una especie mexicana y diversas variedades nuevas. La exacta distribución geográfica queda fijada con la citación de ejemplares de herbario seleccionados. Se incorporan resultados de recientes investigaciones citogenéticas, palinológicas, quimiotaxonómicas y serológicas.

CHROMOSOME NUMBER AND ITS SIGNIFICANCE IN BATIS MARITIMA (BATACEAE)

PETER GOLDBLATT *

THE SMALL AND VERY DISTINCT family Bataceae comprises two species of succulent halophytic subshrubs, widespread in littoral zones of the tropics and subtropics, with one species, *Batis maritima* L., found in the New World (and naturalized in the Hawaiian Islands) and a second species, *B. argillicola* van Royen, in New Guinea. The low-growing plants have opposite leaves and either distinctive conelike male or female inflorescences borne on separate plants or solitary, unisexual flowers borne on the same plant. The flowers are much reduced and tetramerous and are subtended either by bracts or by leaves in the case of *B. argillicola*, which has solitary flowers. The affinities of the very peculiar Bataceae have long puzzled botanists, and the family has been allied at various times with an unusually large and varied number of different groups (McLaughlin, 1959; Mabry & Turner, 1964). Most recently (Dahlgren, 1975; Goldblatt *et al.*, 1976) the family Bataceae has been placed with the Australian Gyrostemonaceae in the order Capparales, a treatment suggested mainly by chemical evidence; however, a relationship to the Gyrostemonaceae is strongly supported by pollen morphology. Determination of the chromosome number in the family was undertaken with the hope that this knowledge would contribute to an understanding of the relationships of Bataceae.

CYTOLOGY

Plants of *Batis maritima* collected in the wild were grown at the Missouri Botanical Garden. A potting medium of pure sand kept completely water-saturated proved suitable, and the plants grew rapidly, producing an abundance of roots.

Root tips were pretreated in 0.003M hydroxyquinoline for four hours, then fixed in acetic alcohol. After hydrolysis in 10% HCl at 60°C for five minutes, root tips were squashed in lacto-propionic orcein.

Batis maritima L. $2n = 22$, Belize, Belize City, tidal flats near St. Josephs College, *Dwyer 12370* (MO); $2n = 22$, U.S.A., Florida, Hillsborough County near Apollo Beach, *Hilsenbeck & Hilsenbeck 627* (USF).

The chromosomes of *Batis maritima* are fairly small, in the 1–2 μm range, but were very clearly stained and well spread out by the treat-

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ment described above. The diploid number of $2n = 22$ is almost certainly correct for the species, although occasionally one or two satellite-like structures, which were about one-third the size of the smaller chromosomes and always located close to larger chromosomes, were observed. This confirms Fulcher's (1972) record of $n = 11$, a count unknown to me at the time this study was undertaken, and contrasts notably with Engel and Schmidt's (1972) count of $2n = 18$ for plants collected in Colombia. It seems probable that either Engel and Schmidt's count is only approximate or an error was made in the identification of their material. A request for the loan of the voucher to check the latter possibility has to date evoked no response.

DISCUSSION

The family Bataceae has been allied with such varied groups as Empetraceae, Buxaceae, Polygonaceae, and Juglandaceae (McLaughlin, 1959), but the most serious consideration has been given to possible relationships with the Amentiferae, particularly Salicaceae (Wettstein, 1935), with the Centrospermae, notably Chenopodiaceae and Amaranthaceae (Hutchinson, 1959; Buxbaum, 1961; Takhtajan, 1969), and most recently with the order Capparales (Dahlgren, 1975).

Most modern phylogenetic treatments, however, have tended to stress the uniqueness of the family, placing it in its own order as did, for example, Melchior (1964), who placed the Batales between the Papaverales and the Rosales, and Cronquist (1968), who placed it between the Caryophyllales and Polygonales, the latter still implying distant affinities with the Centrospermae. Thorne (1968) also admitted the Batales to his Chenopodiiflorae; more recently (1973), however, he has indicated that he believes the order to be unrelated to Chenopodiiflorae, although he does not not suggest an alternative relationship. Dahlgren (1975) assigned Bataceae to his Violanae, a superorder comprising Violales, Tamaricales, Salicales and Capparales, and he suggested placing the Bataceae either in the Capparales or in a separate order, the family in both cases being closely associated with the Australian Gyrostemonaceae. Dahlgren's treatment is supported by Goldblatt *et al.* (1976) mainly on the basis of chemical evidence.

Seen against this rather conflicting background, the chromosome number of $n = 11$ in *Batis maritima* appears to be highly significant, particularly with reference to the Centrospermae and the Salicaceae. The latter, with the distinctive base number of 19, is seen as an unlikely relative of the Bataceae, and any possibility of this relationship can be discounted in the light of much other evidence.

The most important base number in the order Centrospermae is 9 (Raven, 1976), and this is clearly basic in Phytolaccaceae and Chenopodiaceae, the latter frequently associated with *Batis*. Within the Centrospermae, higher base numbers occur in the Basellaceae ($x = 12, 11$) and Cactaceae ($x = 11$), while abundant aneuploidy in the Amarantha-

ceae, Portulacaceae, Nyctaginaceae, and Caryophyllaceae makes it difficult to ascertain base numbers. However, Bataceae, with $x = 11$, is clearly discordant with the group of families in the Centrospermae with which it is most often associated.

In the light of phytochemical studies (Chang & Mabry, 1973; Mabry & Turner, 1964) and recent palynological and ultrastructural evidence (Goldblatt *et al.*, 1976), the family Bataceae is now seen as almost certainly misallied with the Centrospermae. *Batis* has plastids containing normal starch grains in sieve tubes and not the peculiar so-called P-type sieve tube plastids of the Centrospermae (Behnke & Turner, 1971). Phytochemical data also support the exclusion of the Bataceae from the Centrospermae (Goldblatt *et al.*, 1976), with the discovery (Ettlinger *fide* Goldblatt *et al.*, 1976) of glucosinolates in the family.[1] This evidence provides support for Dahlgren's placement of *Batis* in the Capparales, together with the mustard oil families. In addition, *Batis* has very unusual pollen grains of a type unknown in the centrospermous families (Erdtman, 1952; Prijanto, 1970a) but very similar to that of the Gyrostemonaceae (Prijanto, 1970b).

The placement of *Batis* in or close to the Capparales (Violanae) apparently is supported by the chromosome data, $x = 10$ and 11 being common in this order and probably basic (Raven, 1976), while $x = 11$ or 12 is the most likely basic number in the Violales. Dahlgren associates Bataceae particularly with the Australian Gyrostemonaceae, which have been shown to have $n = 14$ (Keighery, 1975; Goldblatt *et al.*, 1976). These two families do not seem particularly closely related on either cytological or morphological grounds, having most notably very similar and unusual pollen grains (Erdtman, 1952; Prijanto, 1970a, 1970b; Nowicke, pers. comm.) which are strikingly discordant with the Centrospermae although also with most members of the Capparales (Erdtman, 1952; Nowicke, pers. comm.). The two families together, however, seem closely allied to Capparales on the basis of the occurrence of glucosinolates in both and myrosinase in *Batis maritima* (Schraudolf *et al.*, 1971; Wagenitz, 1975).

In summary, it can be said that the chromosome number of *Batis maritima* contributes to the weight of evidence excluding Bataceae from Centrospermae and Salicaceae. Similar base numbers occur in Capparales and in *Batis*, but the Gyrostemonaceae, suggested as the closest ally of Bataceae in a Capparalean alliance, has $x = 14$, and this in itself provides no support for the supposed relationship between Bataceae and Gyrostemonaceae. The number $n = 11$ in *Batis* is, however, consistent with basic chromosome numbers in Capparales and in the Violanae in general. Of course, the chromosome number of *B. argillicola* is still unknown, and until this is determined, no further conclusions can be drawn.

[1] *Batis* has been analyzed for betacyanins and betaxanthins, characteristic of many, but not all, centrospermous families (Mabry & Turner, 1964), but no trace of either was reported. The absence of these two pigments, however, indicates nothing in itself about the relationships of Bataceae.

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* Cited in error as "var. subinermis" rather than as "forma subinermis."

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